SPACE USE DURING PARTURITION INFLUENCES CARIBOU CALF SURVIVAL IN NEWFOUNDLAND

by

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ABSTRACT

In social species the choice to aggregate in space is hypothesized to affect survival and reproduction (i.e., fitness). My research addresses the hypotheses provided by the Ideal Free Distribution (IFD) and the Geometry of the Selfish Herd (GSH) that could explain how an individual can maximize their fitness by choosing to aggregate, or choosing to disaggregate during the period where offspring are most vulnerable. I used woodland caribou (*Rangifer tarandus*) in Newfoundland as a model system to test the influence of aggregation on calf survival. In support of this effort, I employed a new movement-based approach to measure parturition and calf survival for adult females. I found empirical support for both the IFD and GSH frameworks and introduce an innovative movement-based approach to inferring parturition and neonate survival in caribou.

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LIST OF ABBREVIATIONS AND SYMBOLS

ΔAIC – Change in Akiake's Information Criteria

AIC – Akiake Information Criteria

CDF – Cumulative distribution function

DOD – Domain of danger

Fogo – Fogo Island herd

GLMM – Generalized linear mixed model

GPS – Global positioning system

GSH – Geometry of the Selfish Herd

IBM – Individual-based model

IFD – Ideal Free Distribution

KDE – Kernel density estimate

MR – Middle Ridge herd

NN – Nearest neighbour

PBM – Population-based model

TDAM – Three-day average movement rate

VHF – Very high frequency

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CHAPTER 1: GENERAL INTRODUCTION

1.1 Animal aggregation

The degree of sociality in many species varies throughout the year from highly dispersed to densely aggregated, particularly during the breeding season. Aggregation is the tendency for animals to group together in space, and in social species the choice to aggregate is hypothesized to carry a fitness trade-off. Animals in groups can benefit from information transfer about resources (Giraldeau and Caracao 2000), reduced predation risk through dilution and confusion effects (Lehtonen and Jaatinen 2016), increased chance of finding a mate (Ward and Webster 2016), and the capacity to cope with extreme environmental conditions (Gilbert et al. 2010). Conversely, the costs associated with aggregating include competition for both resources and predator free space (Bateman et al. 2012); easier detection by predators (Hebblewhite and Pletscher 2002; but see Fryxell et al. 2007; Ioannou et al. 2011); and increased transmission of disease (Vander Wal et al. 2012; Proffitt et al. 2015). Given that aggregations provide benefits as well as costs to individuals, it is therefore important to appreciate the extent to which aggregation affects components of fitness, such as survival or reproductive success.

Birthing aggregations, where animals aggregate in large groups shortly before parturition and then give birth in synchrony, are hypothesized to improve an individual's fitness by improving reproductive success (Ims 1990). It takes a finite amount of time for a predator to capture and subdue prey, and the prey species can capitalize on this constraint by synchronizing emergence and effectively overwhelm a predator's ability to consume prey thereby reducing the overall number of prey taken from the population

(Ims 1990; Krause and Ruxton 2002). For example, green turtles (*Chelonia mydas*) synchronize hatching on beaches (Santos et al. 2016), Adélie penguins (*Pygoscelis adeliae*) form birthing colonies (Ainley et al. 2005), and fruiting plants synchronize seed emergence (Janzen 1971). In all of these examples there is considerable variation in juvenile survival but little variation in adult survival. Thus, variation in adult fitness is comprised primarily of the variation in their reproductive success. Birthing aggregations represent opportunities for natural selection on social aggregation behaviour as variation in the degree of social aggregation affects variation in fitness.

Reproductive success, defined as the survival of offspring to the point where they too can produce offspring, is an important component of fitness irrespective of birthing strategy, yet measuring reproductive success is especially important when animals have birthing aggregations as they purportedly cause an increase in reproductive success of the group. Therefore a measure of reproductive success is required during birthing to quantify the relationship between social aggregation behaviour and variation in reproductive success and thus, variation in fitness. Methods for assessing reproduction in wild animals include counting egg clutch sizes, egg success, and nest success in birds (Murray 2000), flying aerial herd composition surveys during the calving season in ungulates, (Whiting et al. 2012), and more invasive techniques such as serum progesterone tests on blood samples taken from captured animals (Wittmer et al. 2005). The challenge with many of these techniques is that they cannot be done remotely, and can be prone to non-representative sampling biases (Ellington et al. 2017).

1.2 A movement-based approach to inferring parturition and survival

Significant life history events, such as parturition, correspond with a change in movement behaviour in many wildlife species. With the advent of high-resolution Global Positioning System (GPS) technologies researchers can now track animal movements almost continuously, providing information to test finer-scale behavioural and spatial hypotheses about wildlife populations (Kays et al. 2015; Wilmers et al. 2015). Ecologists and wildlife managers can now ascertain measures of individual fitness (i.e., survival and reproduction) using a movement-based approach. For example, individual mortality events can be determined accurately and with confidence when transmitters are equipped with mortality sensors (Dinsmore et al. 2002; Murray 2006; Murray and Patterson 2006). Furthermore, researchers have been able to estimate the timing of parturition events using movement data (Vore and Schmidt 2001; Carstensen et al. 2003; Ciuti et al. 2006; Long et al. 2009) and more recently, infer neonate survival using only the movement rates of maternal females (DeMars et al. 2013). A movement-based approach to ecology and wildlife research that relies on maternal GPS data, represents a way to actively and retroactively collect important data on fitness measures, such as parturition and neonate survival, eliminating the need for techniques that may be financially costly, and invasive to vulnerable demographics (i.e., neonates) such as using biotelemetry collars.

A movement-based approach may be an effective way to measure offspring survival in ungulates because parturition in ungulates is generally associated with a steep reduction in movement rate (van Beest et al. 2013) and movement rate slowly increases as calves become more mobile. Previous methods for assessing reproduction status in wild ungulates have included herd composition surveys (HCS) during the calving season

(Whiting et al. 2012), and biotelemetry of collared calves. These data collection methods can be invasive and/or prone to biases; particularly non-representative sampling biases from telemetry and unequal detectability biases from the HCS (Ellington et al. 2017). A movement-based approach to inferring parturition and neonate survival has the potential to overcome non-representative sampling biases from telemetry particularly since it relies on maternal GPS telemetry data, potentially replacing collaring of neonates, while still producing an individual-based metric of fitness.

1.3 The ungulate model

Many ungulate species such as bighorn sheep (*Ovis canadensis*) wildebeest (*Connochaeres raurinus*), and caribou (*Rangifer tarandus*), choose to aggregate seasonally and give birth in synchrony (Bergerud 1975; Estes 1976; Whiting et al. 2012). Female ungulates generally trade off foraging opportunities for decreased predation risk (Fryxell 1991) although there is also evidence to suggest that some ungulates reduce the cost of this fitness trade-off by synchronizing parturition with seasonal productivity (Festa-Bianchet 1988; Bowyer et al. 1998). In ungulates, adult survival is generally not as variable, while juvenile survival varies considerably, particularly in the first weeks of life (Gaillard et al. 2000). Thus, contributions to an adult's fitness are largely determined by its reproductive success during this early period post-parturition (Gaillard et al. 2000). Furthermore, the degree of aggregation varies seasonally, with female-offspring herds being more tightly aggregated during parturition and during the calf-at-heel period, compared to the rest of the year (Bergerud 1975). Ungulate birthing aggregations therefore represent an opportunity for selection on aggregation behaviour, as variation in both aggregation behaviour and variation in fitness exist.

1.4 Thesis overview

My thesis aims to quantify the fitness effects of space use during and post-parturition using woodland caribou (*Rangifer tarandus caribou*) in Newfoundland as a model system. First in Chapter 2 I quantify a fitness metric by applying a new movement-based model that uses GPS inter-fix step length of adult female caribou to infer parturition event and neonate survival. In Chapter 2 I extend the use of the model after assigning parturition and calf mortality status by examining herd-wide distributions of parturition date, calf mortality date, and survival. In Chapter 3 I bring together two silos of research on evolutionary strategies for space use: the Geometry of the Selfish Herd and Ideal Free Distribution and use the combined framework to explain how aggregation on calving grounds by female caribou influences calf survival. In Chapter 4 I discuss the management implications of movement-based approaches to ecology and wildlife research, and of understanding seasonal aggregation and space use behaviours that ultimately affect individual fitness through offspring survival.

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1.6 Co-Authorship Statement

Chapter 2 of this thesis was co-authored with Drs. E. Hance Ellington, Keith P. Lewis and Eric Vander Wal and Chapter 3 of this thesis was co-authored with Dr. Eric Vander Wal. I was the principal contributor to the design, data analyses and manuscript preparation for all chapters of this thesis. For Chapter 2 Dr. Ellington provided assistance with data analyses and feedback during manuscript preparation, and Dr. Lewis contributed helpful feedback in design and writing. Dr. Vander Wal provided critical guidance and feedback from the initial study design through to manuscript preparation for both chapters.

Chapter 2 is currently accepted for publication in *PLoS One* and Chapter 3 will be submitted to *Oecologia* as a Concepts, Reviews and Syntheses article upon thesis completion. Thus it was necessary to repeat some information from Chapter 1 in the study scope and objectives in both Chapters 2 and 3 and formats between the two chapters may differ slightly to conform to target journal guidelines.

CHAPTER 2: IMPLEMENTING A NOVEL MOVEMENT-BASED APPROACH TO INFERRING PARTURITION AND NEONATE CARIBOU CALF SURVIVAL

2.1 Abstract

In ungulates, parturition is correlated with a reduction in movement rate. With advances in movement-based technologies comes an opportunity to develop new techniques to assess reproduction in wild ungulates that are less invasive and reduce biases. DeMars et al. (2013, Ecology and Evolution 3:4149–4160) proposed two promising new methods (individual- and population-based; the DeMars model) that use GPS inter-fix step length of adult female caribou (*Rangifer tarandus caribou*) to infer parturition and neonate survival. Our objective was to apply the DeMars model to caribou populations that may violate model assumptions for retrospective analysis of parturition and calf survival. We extended the use of the DeMars model after assigning parturition and calf mortality status by examining herd-wide distributions of parturition date, calf mortality date, and survival. We used the DeMars model to estimate parturition and calf mortality events and compared them with the known parturition and calf mortality events from collared adult females (n = 19). We also used the DeMars model to estimate parturition and calf mortality events for collared female caribou with unknown parturition and calf mortality events (n = 43) and instead derived herd-wide estimates of calf survival as well as distributions of parturition and calf mortality dates and compared them to herd-wide estimates generated from calves fitted with VHF collars (n = 134). For our data, the individual-based method was effective at predicting calf mortality, but was not effective at predicting parturition. The population-based method was more effective at predicting

parturition but was not effective at predicting calf mortality. At the herd-level, the predicted distributions of parturition date from both methods differed from each other and from the distribution derived from the parturition dates of VHF-collared calves (log-ranked test: $\chi^2 = 40.5$, df = 2, $p < 0.01$). The predicted distributions of calf mortality dates from both methods were similar to the observed distribution derived from VHF-collared calves. Both methods underestimated herd-wide calf survival based on VHF-collared calves, however, a combination of the individual- and population-based methods produced herd-wide survival estimates similar to estimates generated from collared calves. The limitations we experienced when applying the DeMars model could result from the shortcomings in our data violating model assumptions. However despite the differences in our caribou systems, with proper validation techniques the framework in the DeMars model is sufficient to make inferences on parturition and calf mortality.

2.2 Introduction

Significant life history events correspond with a change in movement behavior in wildlife species. For example, parturition in ungulates is generally associated with a steep reduction in movement rate [1] and movement rate slowly increases as offspring become more mobile. Due to recent advances in statistical techniques and GPS technologies [2,3], researchers have been able to not only estimate the timing of parturition events using movement data [4–7] but also to assess calf survival based on the movements of adult female caribou [8]. However, the transferability of new methods may be limited by assumptions from the system in which the model was built. Recently, a promising advance in estimating parturition and neonate calf survival using movement data of adult females was developed for sedentary caribou (*Rangifer tarandus caribou*) herds in central British Columbia, Canada by DeMars et al. [8] (hereafter "the DeMars model"). Across their circumpolar distribution caribou exhibit variation in their movement behaviors, which may differ from those, exhibited in central British Columbia.

Previous methods for assessing reproduction in wild ungulates have included herd composition surveys (HCS) during the calving season [9], serum progesterone tests on captured animals [10], and vaginal implant transmitters [11]. Estimates of herd-wide calf survival can be made using recruitment rates from HCS [12] or from survival analysis using telemetry. These data collection methods can be invasive and prone to biases; particularly, non-representative sampling biases from telemetry and unequal detectability biases from the HCS [13]. DeMars et al. [8] proposed both an individual-based (IBM) and population-based (PBM) method for determining parturition and calf mortality events using adult movement data. The IBM uses movement models of GPS inter-fix distances

(i.e., step length) of adult females and maximum likelihood estimation to infer parturition and calf mortality events [8]. The PBM uses a sample of adults with known parturition and calf mortality events to generate population level parturition and mortality movement thresholds based on inter-fix step length, which is subsequently used to identify the occurrence of parturition and calf mortality events in the larger adult GPS telemetry dataset [8]. Both methods are less invasive to neonate calves and have the potential to be more cost-effective than traditional methods as they rely solely on adult GPS telemetry data. Moreover, the DeMars model permits retrospective analysis to assess vital statistics (e.g., parturition and calf survival), increasing the value of previously collected GPS telemetry data. Despite these benefits, few studies have inferred parturition and survival in neonatal ungulates using the DeMars model (but see [14]). Furthermore, the model has not been independently validated.

Mirroring global caribou (*Rangifer tarandus*) declines [15], woodland caribou (*R. t. caribou*) population abundance has declined by more than 60% in the last 10 years in Newfoundland, which led the Committee on the Status of Endangered Wildlife in Canada to designate the caribou populations in Newfoundland as “Special Concern” [16,17]. In many ungulate systems including Newfoundland calf mortality is often the basis for initial population decline [18]. Given the recent population decline, woodland caribou demographics have been extensively monitored in Newfoundland. This presents an opportunity to retrospectively apply the DeMars model in this system. DeMars et al [8] outline two key assumptions regarding their model: 1) the assumption of movement independence among females and 2) the assumption of data quality. The caribou herds DeMars et al [8] used to build their model are considered sedentary in that they do not

make long-distance migrations, and are assumed to move independently of one another and are not subject to group dynamics. When using their methods, DeMars et al [8] indicate that for data sets with fix success rates of <90%, estimates of offspring survival may be unreliable and thus assumes that data quality is sufficiently high to make accurate model inferences.

Our aim is to apply the DeMars model to two caribou populations in Newfoundland, Canada, where mother-offspring data were available and movement behaviors of caribou might violate the assumptions of the DeMars model. The purpose of our study was two-fold: 1) apply these two new methods to different ungulate populations and study systems that may violate model assumptions to determine if inferences are possible; and 2) examine the accuracy of our data to generate herd-wide survival estimates and distributions of parturition and calf mortality dates. We expect the DeMars model will be transferable in at least some capacity for both test populations of caribou in Newfoundland. However, the DeMars model will likely make more accurate inferences when applied to the more sedentary of the two populations that are similar in behaviour to the herds DeMars et al [8] used to build their model.

2.3 Materials and methods

2.3.1 Study area

I conducted my study in Newfoundland, a 108 860 km^2 island in eastern Canada (47°44 N, 59°28 W to 51°44 N, 52°38 W), with a humid–continental climate and ample year-round precipitation. The landscape consisted of coniferous and mixed forests of balsam fir (*Abies balsamea*), black spruce (*Picea mariana*) and white birch (*Betula papyrifera*), as well as bogs, lakes, and barren rock. My analysis focused on caribou in

two separate herds: Middle Ridge and Fogo Island. Middle Ridge is located on the south central portion of Newfoundland and Fogo Island (237 km^2) is situated off the northeastern coast of Newfoundland. The landscape that these two herds occupy is broadly similar, however, Fogo Island is separated from mainland Newfoundland by approximately 12 km and the Fogo Island herd is sedentary and does not display the same migration pattern as the Middle Ridge herd.

2.3.2 Overview

First, I compared estimates of parturition and calf mortality events generated using the DeMars individual based model (IBM) and population based model (PBM) to adults (n = 19) with known parturition and calf mortality events from two different woodland caribou herds in Newfoundland. Second, I compared herd-wide calf survival estimates and distributions of parturition and calf mortality dates using both the DeMars IBM and PBM from a large multi-year (n = 43) adult telemetry dataset to the herd-wide survival estimates and distributions of parturition and calf mortality dates derived from concurrent calf telemetry data (n = 134). This required 1) GPS telemetry data from adult female caribou with known and unknown parturition and calf mortality events; 2) herd-wide estimates of calf survival; 3) herd-wide estimates of the distribution of parturition date; and 4) calf mortality dates from collared calves (Fig 1).

2.3.3 Caribou telemetry and observational data

Adult female caribou were captured using a net gun or darted using the immobilizing agent Carfentanil. Females were not captured or immobilized during the calving season to avoid transferring immobilizing drugs to calves. GPS 4400M collars (1240g, Lotek Wireless Inc., Newmarket, ON, Canada) were deployed on 43 adult

females in the Middle Ridge (MR: 2009-2013) herd and 9 adult females in the Fogo Island (Fogo: 2015) herd. Sampling adults followed typical large mammal procedures, i.e., haphazard or convenient sampling. A GPS fix was attempted every two hours from May 21 – July 31 and every five hours for the remainder of the year for females in the MR herd and every two hours year-round for females in the Fogo herd. The status of parturition and calf mortality was known for all 9 collared adult females in the Fogo herd (using direct observation; see below) and for 10 of the collared adult females in the MR herd (via paired VHF-collared calves; see below). Pregnancy status was visually determined for the 19 adult females upon capture.

From 2009 – 2013, caribou calves from the MR herd were located from helicopter and captured on foot during the calving season. Most calves were captured <5 days after birth. Ear-tags and expandable 200g VHF radio-collars (Telemetry Solutions, Concord, CA, USA) were deployed on 134 calves in the MR herd; this included 10 calves that were paired with GPS-collared adult females in 2009. These collars were under the recommended 5% of the individual's body mass [19]. Calves were visually relocated by helicopter within 24 hours of initial capture to ensure they had re-bonded with their mothers. Passive transfer status was not determined for each calf upon capture. Survival was monitored daily during the first week of post capture, and then at least twice a week through August. When a neonatal mortality signal was detected, the collar was located aerially and field crews located calf remains and assigned cause of death based on remains and site conditions (see [20] for full details).

We assessed caribou parturition and calf survival for the Fogo herd in 2016 through visual observation. We located each collared adult female on foot every week ($\bar{x}$ = 7;

range = 1-19 days) from 24 May 2016 until 30 June 2016 and then every three weeks ($\bar{x}$ = 25; range = 17-34 days) from 1 July 2016 until 30 July 2016. We located each female at least three times and we confirmed that a calving event occurred when a female was observed with a calf. We continued locating the adult females after calving to assess calf survival until four weeks of age. We continued to track and observe adult females after calf loss was suspected to confirm calf status. As none of these females were subsequently observed with a calf, we assumed that the true status of the calf was known (Memorial University of Newfoundland Animal Care and Use Committee 16-03-EV).

2.3.4 Estimating parturition and calf mortality events

2.3.4.1 DeMars individual-based method

Following DeMars et al. [8], our IBM for parturition and calf mortality events used three *a priori* models representing the three possible states of a female ungulate during calving season: 1) no parturition; 2) calf survived to four weeks old; and 3) calf mortality occurred before the calf was four weeks old (Fig 2). In the model, "no parturition", the mean step length remained constant over time. In the other two models, an event (i.e., parturition or calf mortality) was represented by an abrupt change in the mean step length: a decrease in mean step length represented parturition and an increase represented calf mortality. Thus, in the model, "calf survived to four weeks old", mean step length dropped abruptly, creating a breakpoint at calving, followed by an increase in mean step length with a slope equal to the ratio between the scale parameter and the number of step lengths required for the calf to reach adult movement rates. Conversely, in the model, "calf mortality occurred before four weeks old", mean step length dropped abruptly, creating a break point at parturition, followed by an increase in mean step length

with a slope equal to the ratio between the scale parameter and the number of step lengths required for the calf to reach adult rates of movement. This slope, however, was interrupted by an abrupt increase in mean step length to the original mean step length of the adult female at the point of calf mortality [8]. All three of the *a priori* models assumed that step length was exponentially distributed and should differ only in the scale parameter (i.e., mean step length). Calf status was assessed up to four weeks as calf mobility after four weeks begins to approach adult movement rates [8].

We screened and removed any erroneous data points arising from unrealistic movement patterns following Bjørnerass et al. [21]. We globally removed 6% of fixes from MR and 10% from Fogo. We further rarefied the datasets to exclude the top 1% of step lengths for each individual, which are thought to be associated with calf capture or predator avoidance behavior [8]. After rarefication, the mean per-collar fix rate (number of successful fixes per number of attempts; [22]) was 80% (range: 53-93%). MR appeared to have a higher mean per-collar fix rate (90%, range: 85-93%) than Fogo (80%, range: 53-87%). Following DeMars et al. [8], we used only step lengths calculated from successive GPS fixes. We used a visual examination of the distributions of step lengths for all 19 calf-cow pairs to determine that the step lengths were exponentially distributed (S1 Appendix). We then generated the IBM for the 10 adult females with known calf status from the MR herd in 2009 and the 9 adult females with known calf status from the Fogo herd in 2016. We present graphical representation of step lengths for all 19 adult females with known calf status in S1 Appendix. We then fit the data to each *a priori* model and determined the most supported model using Akaike's Information Criterion (AIC; [23]). We tested our IBM over the time interval 21 May – 30 July for 43

individuals in the MR herd and 8 individuals in the Fogo herd. We tested our IBM over the time interval 30 May – 30 August for one individual to account for a record-late birth in the Fogo herd in 2016 [24]. After applying the IBM to our data, we then compared the predicted calf survival outcomes generated from the IBM with the known outcomes for each female.

2.3.4.2 DeMars population-based method

The PBM used population level event thresholds (parturition and calf mortality) of 3-day average movement rates (TDAM) in a 3-day moving window analysis to predict calving and calf survival events. Following DeMars et al. [8], to define the parturition threshold, we first generated a distribution of TDAM rates for 3 days post-calving for females who had calves survive to 1 week. We then converted the distribution of movement rates to a kernel density estimate (KDE), which represented the population-level distribution of TDAM rates 3 days post-calving. We transformed this KDE into a cumulative distribution function (CDF) that represented the proportion of the population expected to move at or below this threshold. We then took the 99.9% quantile of the CDF as the parturition threshold; we assumed that movement below this threshold during the moving window analysis indicated calving [8]. To more accurately reflect the true 3-day post-parturition window and thus improve the biological accuracy of the parturition threshold, we estimated parturition date as 1 day prior to calf captures. Capture date, 3 days prior, and 2 days prior were also tested but were less accurate overall (data not shown).

To generate the calf mortality threshold from a distribution of TDAM rates we followed the same methods outlined above that were used to generate the parturition

threshold, this time for 2-4 weeks post-parturition for females who had calves survive to 4 weeks old. The 99.9% quantile of CDF from this data represented the maximum TDAM rate of a female with a calf up to four weeks old (i.e., calf mortality threshold); we assumed that movement above this rate indicated calf mortality [8].

Prior to calculating the parturition and calf mortality thresholds, we rarefied the data to exclude the top 1% of step lengths. We assumed this removed any step lengths that could have been associated with calf capture or predator avoidance [8]. We generated the parturition and calf mortality thresholds (in the manner described above) in program R [25] using a function provided by DeMars et al. [8]. We modified the function used to generate the parturition thresholds to reflect the variation in TDAM rates within our data (S2 Appendix).

We generated PBM estimates for each herd (MR, Fogo) and the combined herds using the 19 adult females with known parturition and calf mortality events. The PBM required a subset of the population that had experienced both parturition but not calf mortality to generate event thresholds – there were 10 adult females that fit this description (7 in MR and 3 in Fogo). To introduce stochasticity and prevent sampling bias, we iteratively sampled all possible combinations of 5 from the 9 adult females across both herds (n = 126) and all possible combinations of 4 from the 7 adult females in MR (n = 35; i.e., k-fold) for generating event thresholds. The iterative sampling technique was not possible for the Fogo herd as only 3 of the 9 collared females could be used to calculate the calving and calf loss thresholds. This included the female with the record-late birth outside of the calving season [24], which we chose to exclude since the female may not be representative of the whole herd. Therefore, we had only one estimate of

event thresholds for the Fogo herd generated using 2 out of 9 collared females. Using these event thresholds, we then compared the PBM-based predictions of parturition and calf mortality events to the known status of all 19 adult females across both herds and for the MR and Fogo herds separately. We considered the prediction conclusive when the proportion of occurrence was ≥ 0.8 otherwise the prediction was inconclusive.

2.3.5 Estimating herd-wide survival, parturition, and mortality date distributions

To generate herd-wide estimates of survival and distributions of parturition and calf mortality dates, we applied both the DeMars IBM and PBM to the 43 GPS-collared adult females from MR. We generated event thresholds required for the PBM using the 7 adult females from the MR herd that had experienced both parturition and calf mortality events. We generated density distributions of the estimated parturition dates and mortality dates derived from the IBM and the PBM. We also converted the estimated calf parturition and mortality events from the IBM and PBM into Kaplan-Meier survival probability curves using the survival package [26] in R. Following Ellington et al. [13], we generated herd-wide survival curves and parturition and mortality date distributions from the 134 VHF-collared calves from the MR herd and compared them to survival curve and distributions generated using the DeMars IBM and the PBM. The VHF collaring date was used as a proxy for parturition dates. Calves were collared during a 1-3 day period at the suspected peak of calving season on any given year. In all analyses, we generated IBM and PBM models using both a 2-hour GPS fix time interval dataset and a rarified 4-hour GPS fix time interval dataset (to reproduce the methods used by DeMars et al. [8]).

2.4 Results

I found that the predictions from the DeMars model for 2-hour time interval were more accurate compared to the 4-hour time interval and have chosen to present the overall results based on the 2-hour time series. The 4-hour time series can be found in Appendix C.

2.4.1 Estimating parturition and calf mortality events

2.4.1.2 DeMars population-based method

The DeMars IBM failed to definitively distinguish (i.e., ΔAIC > 2 for the most parsimonious model) a parturition and calf mortality status for 2 out of 9 adult females from the Fogo herd and definitively distinguished parturition and calf mortality status for the remaining 7 adult females. In both cases where the IBM failed to distinguish the most parsimonious model, the models "calf survived to four weeks old" and "calf mortality occurred before calf was four weeks old" were competing. In one case, parturition occurred, and the calf survived to four weeks (ΔAIC = 1.23), and in the other case parturition occurred and calf mortality occurred before four weeks (ΔAIC = 1.94). In these cases I considered the IBM method successful in predicting parturition but inconclusive in predicting mortality events. The DeMars IBM definitively distinguished (though not always correctly) a parturition and calf mortality status for all 10 adult females from the MR herd. AIC and ΔAIC values for all 19 individuals can be found in Appendix A (Table A1).

The IBM correctly classified the two adult females who had no parturition event. The IBM also correctly predicted parturition in 7 of 17 adult female caribou in which

parturition occurred (4 of 10 for MR and 3 of 7 for Fogo; Table 2.1). In situations in which parturition occurred but the IBM method failed to predict parturition (n = 10), calf mortality did not occur in 8 of 10 cases (6 of 6 in MR and 2 of 4 in Fogo; Table 2.1). Indeed, the IBM method correctly identified only 1 of 10 adult females in which parturition occurred but calf mortality did not occur (1 of 7 in MR and 0 of 3 in Fogo; Table 2.1). This suggests that the IBM method might perform better at identifying parturition when calf mortality occurs in the first four weeks than when it does not. The IBM method predicted calf mortality in 4 of 7 adult female caribou in which calf mortality occurred (3 of 3 for MR and 1 of 4 for Fogo; Table 2.1).

2.4.1.2 DeMars population-based method

The event thresholds using the PBM were higher in the MR herd than the Fogo herd (parturition: 208 m/hr [range: 146 - 266 m/hr] vs 23 m/hr and calf mortality: 407 m/hr [range: 217 - 567 m/hr] vs 126 m/hr). Perhaps this is not surprising given that the dimensions of the island confine space use patterns of caribou in the Fogo herd. Surprisingly, the event thresholds using the combined MR and Fogo data were higher than the MR event thresholds, perhaps due to larger sample size within the k-fold subset (parturition: 259 m/hr [range: 180 - 296 m/hr] and calf mortality: 460 m/hr [range: 210 - 563 m/hr]).

In general, the PBM performed better for each herd when it used herd-specific event thresholds than when it used event thresholds derived from the combined herds (Appendix A), thus I focus my results on PBM based on herd-specific event thresholds. Because of the iterative process in generating event thresholds for the MR herd, multiple outcomes were generated for each event (parturition, no parturition, calf mortality, calf

survival). The resulting estimates for each event were pooled as proportion of occurrence across all the event thresholds. I considered the prediction conclusive when the proportion of occurrence was ≥ 0.8 otherwise the prediction was inconclusive. Due to small sample size, there was no iterative process in generating event thresholds for the Fogo herd, thus there were no inconclusive predictions.

The PBM correctly predicted parturition status for 16 of 17 females across both herds (15 of 15 parturient and 1 of 2 non-parturient). For one female in the Fogo herd it predicted parturition when parturition did not occur (Table 2.2). The PBM did not predict calf mortality correctly and conclusively; in cases where calf mortality occurred the PBM predicted no calf mortality for 2 out of 4 individuals in the Fogo herd (Table 2.2) and was inconclusive for all individuals (n = 3) in the MR herd (Table 2.2). The PBM predicted calf mortality did not occur in 6 of 8 females where calf mortality did not occur (5 of 7 in MR and 1 of 1 in Fogo; Table 2.2). These results suggested that PBM was more accurate at predicting parturition and the lack of calf mortality than predicting calf mortality, which is opposite to the performance of IBM; the latter was more accurate when predicting parturition with calf mortality than predicting parturition without calf mortality.

2.4.2 Herd-wide survival estimates and distributions of parturition and mortality dates

The predicted distributions of parturition date from the IBM and PBM were different from each other and from the distribution derived from the VHF-collared calves. The IBM predicted that parturition occurred in a wide distribution with only a small peak occurring > 1 week before the observed peak from the VHF-collared calf data, which

suggested a long, diffuse calving season (Figure 2.3a). Conversely, the PBM predicted that parturition occurred in a distribution with a steep peak > 2 weeks before the observed peak from the VHF-collared calf data, which suggested a calving season broadly similar to the observed calving season but with the majority of parturition events occurring much earlier than they have been observed (Figure 2.3a). Among individuals with known parturition events, the IBM predicted parturition dates were within 1 day of the collared date (n = 3; i.e., the IBM method when accurate was highly precise; Appendix A). The PBM method predicted parturition dates that were typically ≥ 6 days underestimated compared to collar date (n = 8; i.e., the PBM method was highly accurate but had a consistent bias; Appendix A)

The predicted distribution of calf mortality dates from the IBM and PBM were broadly similar to the observed distribution from the subset of VHF-collared calves in which mortality occurred prior to 4 weeks of age (Figure 2.3b). The only major discrepancy was that the peak in mortality date occurred slightly earlier using the PBM than the IBM or the observed VHF-collared calves (Figure 2.3b). Among individuals with known mortality events (n = 3), the IBM method identified all mortality events but predicted mortality dates varied (-3 to 10 days difference from actual mortality event; i.e., the IBM method was highly accurate but imprecise). The PBM method identified only two of the three known mortality events and consistently underestimated the mortality date (i.e., the PBM method was less accurate and also had a consistent bias).

Both the DeMars IBM and the PBM estimated lower herd-wide survival than what was observed from VHF-collared calves (log-ranked test: $\chi^2 = 40.5$, df = 2, $p < 0.01$;

Figure 2.4a). The IBM estimated 38 parturition events and 30 mortality events, and the PBM estimated 95 parturition events and 59 mortality events for the 43 females over the 5 years. Out of the 134 VHF-collared calves there were 38 mortality events. However, given the performance of the IBM and PBM when estimating parturition and calf mortality, I generated a survival curve where the PBM was used to identify parturition and the IBM was used to identify mortality (assuming the parturition status identified by PBM). The combined method estimated 97 parturition events and 30 mortality events. Survival rates that I estimated with this combined IBM and PBM method were not statistically different from the 134 VHF collared calves in MR from 2009–2013 (log-ranked test: $\chi^2 = 3.9$, df = 1, $p = 0.05$; Figure 2.4b).

2.5 Discussion

In ungulates, parturition corresponds with an abrupt drop in movement rate [1,27]. This relationship has been used in the past to estimate parturition from movement data with mixed success [1,4,27,28]. DeMars et al. [8] took this relationship further and developed two methods (individual- and population-based; IBM, PBM) to identify neonate calf mortality in addition to parturition for sedentary caribou. We intended to see if the DeMars model will work to assign parturition and calf mortality statuses to adult female caribou for the purpose of survival analysis despite violating the assumptions. In general, the accuracy of both methods was lower for caribou in two herds in Newfoundland relative to what DeMars et al. [8] observed for caribou in British Columbia. Our IBM did not perform well at predicting parturition (particularly if calf mortality did not occur), but performed better at predicting calf mortality. Conversely, our

PBM did not perform well at predicting calf mortality, but predicted parturition with near perfect accuracy. On their own, these methods did not generate accurate herd-wide survival estimates based on VHF-collared calves in Newfoundland. Combined, however, the two methods produced herd-wide survival estimates similar to radio-telemetry.

DeMars et al. [8] developed their original model using sedentary woodland caribou in British Columbia. The sedentary caribou ecotype tend to isolate themselves from other individuals to decrease detection from predators [29], whereas migratory caribou will space away from the distribution of predators and calve in large aggregations [30,31,32]. Thus, sedentary caribou may meet the assumption of independent movement for the DeMars model, but migratory caribou may not. Indeed, the poorer performance of both the IBM and PBM with the migratory caribou of the MR herd (relative to [8]) might be partially driven by violating the assumption of independent movement. Caribou in the MR herd move together to the calving grounds and most individuals arrive at the calving grounds within a few days of each other, even if parturition does not occur at this time. This behavior could have led the PBM to consistently underestimate parturition date both at the individual- and herd-level. The inclusion of a variance-covariance matrix into the model could control for the lack of independent movement in the MR herd.

In terms of movement behavior the Fogo herd was more similar to the sedentary caribou in DeMars et al. [8] than the MR herd. The event thresholds of the PBM for the Fogo herd were comparable to the thresholds from sedentary caribou in British Columbia (parturition: 23 m/h for Fogo 15 m/h for sedentary from British Columbia; mortality: 126 m/hr for Fogo and 187 m/h for sedentary from British Columbia; [8]). However, this similarity did not appear to lead to improved performance; improved performance could

have been masked by low sample size in the Fogo herd (n = 9) and the rate at which visual observations occurred (i.e. early mortalities could have been missed by observers).

While the number of calf-cow pairs is comparable between herds, (10 for MR and 9 for Fogo), the proportion of individuals sampled in the MR and Fogo herds differed considerably. We sampled 10 calf-cow pairs and 43 adult females out of approximately 10 000 individuals in the MR herd compared to 9 calf-cow pairs out of approximately 300 individuals in the Fogo herd. This unbalanced sample size could affect the inferences made from the DeMars model. In particular, we make herd-wide inferences about calf survival using < 1% of the herd for MR compared to 3% of the herd for Fogo. However, it is notable that despite small samples sizes offspring survival analyses generated from the IBM and PBM on GPS collared adult females was comparable to survival analyses derived from calf VHF collars. Additionally, there was less variation in parturition and mortality states in the calf-cow pairs (e.g., no non-parturient females in MR, and 2 calves survived to 4 weeks in Fogo), which meant that we were unable to test the performance of the PBM as rigorously.

Even though both the IBM and PBM did not perform as well using migratory woodland caribou in Newfoundland than for sedentary woodland caribou in British Columbia [8], the way in which performance varied among the two methods was similar. Like DeMars et al. [8], we found that the PBM more accurately predicted parturition and the IBM more accurately predicted calf mortality before four weeks. More specifically, DeMars et al. [8] noted that over 95% of incorrect IBM predictions resulted from adult females with surviving calves being misclassified, which is comparable to our IBM where 92% of incorrect IBM predictions resulted from adult females with surviving calves being

misclassified as non-parturient cows. It is possible that the start date for the time interval over which we tested (May 21) was too close to actual calving period and thus there was insufficient pre-calving data for the IBM to accurately detect parturition. Unfortunately our collars attempted a GPS fix every two 2 hours from May 21 – July 31 and every five hours for the remainder of the year and therefore an extension of the pre-calving interval was not possible. The strengths of the IBM and PBM offset the weaknesses of each method, presenting us with an opportunity to combine both methods to synthesize best-case results. When parturition was predicted using PBM and calf mortality before four weeks was predicted using IBM in the migratory MR herd, the resulting herd-wide estimates of calf survival were not different from those generated using traditional survival analysis of VHF-collared calves (Fig 4).

When a method accurately predicted an event (PBM for parturition and IBM for calf mortality), the precision around date of occurrence was either low (IBM for calf mortality) or consistently biased (PBM for parturition). This imprecision was detectable at both the individual- and herd-level. At the herd-level we compared our IBM and PBM predicted event date distributions to distributions from VHF-collared calves. These distributions have their own limitations, for example parturition dates (as indexed by collaring dates) might not be representative of the entire herd because researchers generally collar animals during a few days of the calving season on any given year due to logistics [13]. This non-representative sampling could have an obvious effect on generating distribution of parturition dates but could also influence the distribution of calf mortality dates, as parturition date influences calf mortality risk in caribou [13]. If precision in predicting event date using the IBM and PBM methods can be improved,

they would represent non-biased herd-wide distributions of these events, which in turn could improve survival analysis using VHF-collared calves.

2.6 Conclusion

A movement-based approach to ecology and wildlife research represents a way to actively and retroactively collect important data on fitness measures, such as parturition and neonate survival, eliminating the need for techniques that may be invasive to vulnerable demographics (i.e., neonates). Ungulate conservation necessitates an understanding of reproduction and survival of juveniles to comprehend the implications on population dynamics [18]. The DeMars model represents an elegant application of movement ecology that may ultimately lead to effective remote quantification of parturition and neonate mortality, thereby adding yet another measure of an important vital rate to a manager's toolbox. Specifically, it allows for a more effective use of scarce financial and human resources, by allowing multiple analyses and study objectives to be derived from the same telemetry dataset. GPS monitoring while assessing neonate survival with the DeMars model may provide a meaningful and financially feasible alternative to monitoring the herd should a population's decline accelerate. By collaring adult females (and using the DeMars model) managers and researchers can assess not only adult survival, habitat use, and spatial ecology, but also neonate survival – a vital demographic rate and fitness correlate for some ungulates [18,33].

The DeMars model has potential to be broadly applicable. For migratory woodland caribou in Newfoundland, the IBM accurately predicted calf mortality but not parturition and the PBM accurately predicted parturition but not calf mortality. Where the DeMars model did not perform as well in our system could be related to violations in the

assumption of independent movement, due to the behavior of the migratory herd, or constraints in data quality or time interval over which the data were assessed. This presents a problem for the transferability of this model to other ungulate species, other caribou ecotypes, or even caribou populations that exhibit variation in movement behavior different from those studied by DeMars et al. [8]. Furthermore, the variation in event threshold was greater between herds than within, which means the PBM will be more accurate when event thresholds are generated for each population or herd with distinct movement behavior. Despite the limitations in our data, by synthesizing the two methods to produce composite results, the DeMars model performed well with migratory woodland caribou in Newfoundland. Thus, if wildlife managers and researchers have a method for validating the DeMars model within their species and system, the DeMars model may be used to make successful inferences on parturition and calf mortality despite violating its assumptions.

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Table 2.1. Parturition and calf mortality status predictions derived from the individual-based method (IBM) from DeMars et al. [8]. Predictions are for 19 calf-cow pairs from Middle Ridge and Fogo Island herd for which calf status was known.

Herd	Status	Observed	IBM Predicted
Middle Ridge	Parturition	10	4
	No Parturition	0	6
	Calf Survival	7	1
	Calf Mortality	3	3
Fogo Island[1]	Parturition	7	3
	No Parturition	2	6
	Calf Survival	3	0
	Calf Mortality	4	1

[1] The individual based method for predicting parturition and calf mortality status was inconclusive (competing models) for two adult females.

Table 2.2. Parturition and calf mortality status predictions derived from the population-based method (PBM) from DeMars et al. [8] for 19 calf-cow pairs from Middle Ridge and Fogo Island herd for which calf status was known. Predictions for Middle Ridge herd were generated by iteratively sampling of 4 out of the 7 females that could be used to generate parturition and calf mortality thresholds for the model and tested the on the remaining 6 individuals for all possible combinations. Predictions were pooled and the proportion of each prediction was calculated for every individual. Predictions for Fogo Island herd were generated by using 2 females that could be used to generate parturition and calf mortality thresholds for the model and tested the on the remaining 7 individuals, thus an iterative process was not possible and there is only one estimate for each event. The 2 individuals used to generate the event thresholds were not included in testing.

	Known Status		**PBM Predictions (proportion of time each status was predicted)**			
ID[1]	**Parturition**	**Calf Survival[2]**	**Parturition**	**No Parturition**	**Calf Mortality[2]**	**Calf Survived[2]**
MR2009a01	Parturition	Survived	1.00	0.00	1.00	0.00
MR2009a04	Parturition	Survived	1.00	0.00	0.00	1.00
MR2009a06	Parturition	Mortality	1.00	0.00	0.49	0.51
MR2009a07	Parturition	Mortality	1.00	0.00	0.46	0.54
MR2009a08	Parturition	Survived	1.00	0.00	0.07	0.93
MR2009a09	Parturition	Survived	1.00	0.00	0.40	0.60

MR2009a25	Parturition	Survived	1.00	0.00	0.20	0.80
MR2009a26	Parturition	Survived	1.00	0.00	0.00	1.00
MR2009a27	Parturition	Mortality	1.00	0.00	0.46	0.54
FO2016002	Parturition	Mortality	TRUE	FALSE	TRUE	FALSE
FO2016005	No Parturition	NA	FALSE	TRUE	NA	NA
FO2016010	Parturition	Mortality	TRUE	FALSE	FALSE	TRUE
FO2016011	Parturition	Survived	TRUE	FALSE	FALSE	TRUE
FO2016012	Parturition	Mortality	TRUE	FALSE	TRUE	FALSE
FO2016014	Parturition	Mortality	TRUE	FALSE	FALSE	TRUE
FO2016015	No Parturition	NA	TRUE	FALSE	TRUE	FALSE

[1]Individual IDs beginning with MR are from Middle Ridge herd and individual IDs beginning with FO are from Fogo Island herd.

[2] When parturition did not occur there was no calf mortality status and when parturition was not predicted there was no calf mortality status predicted.

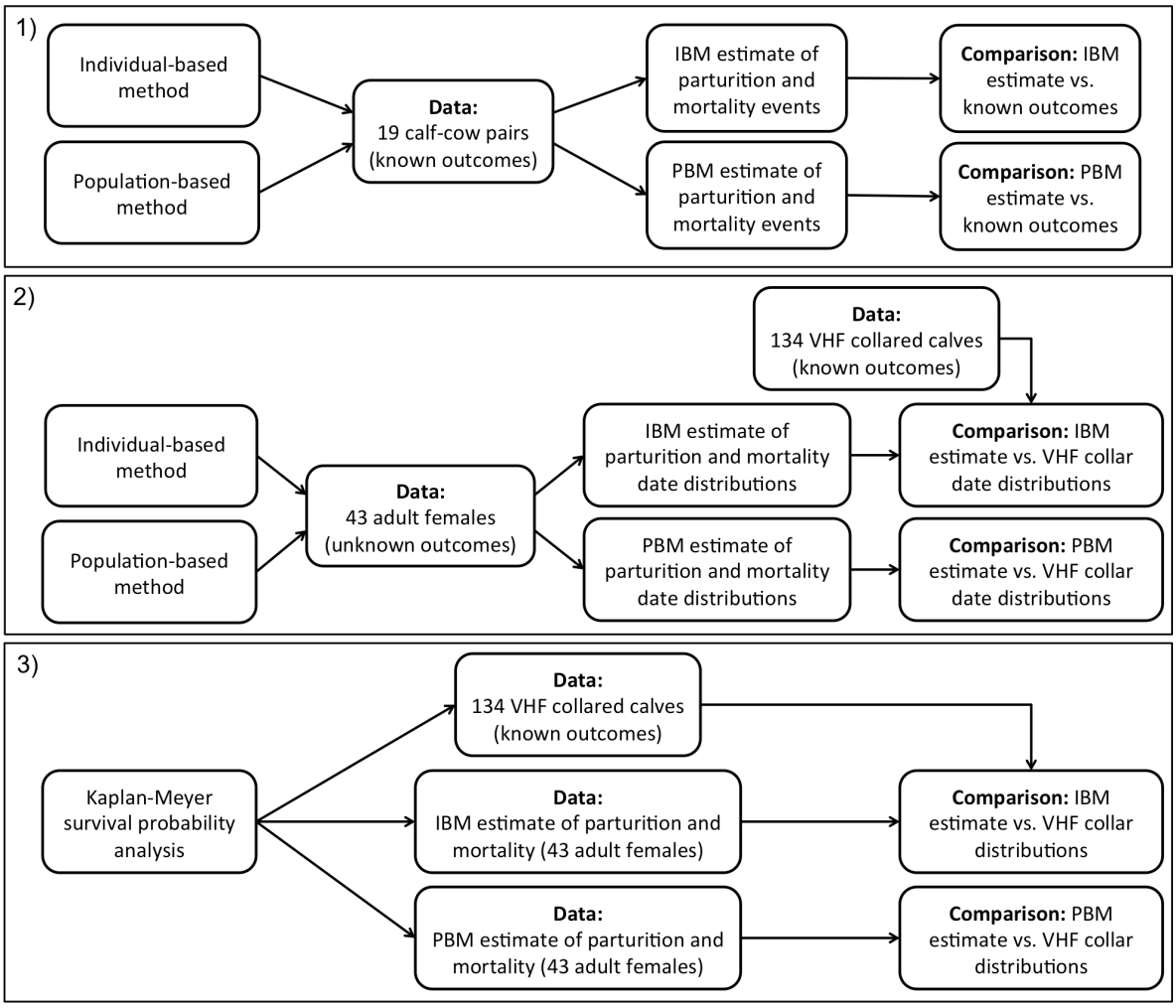

Figure 2.1. Overview of the DeMars model application to two caribou populations in Newfoundland, Canada. We applied the individual-based method and population-based method in three different ways. 1) We estimated parturition and calf mortality events using the two methods to adults (n = 19) with known parturition and calf mortality events from two different woodland caribou herds in Newfoundland. 2) We estimated herd-wide distributions of parturition and calf mortality dates using the two methods and a multi-year (n = 43) adult telemetry dataset and compared those distributions to the herd-wide distributions of parturition and calf mortality dates derived from concurrent calf telemetry

data (n = 134). 3) We generated herd-wide calf survival estimates from Kaplan-Meyer probability curves using the two methods and a multi-year (n = 43) adult telemetry dataset and compared those probability curves to herd-wide survival probability curves derived from concurrent calf telemetry data (n = 134).

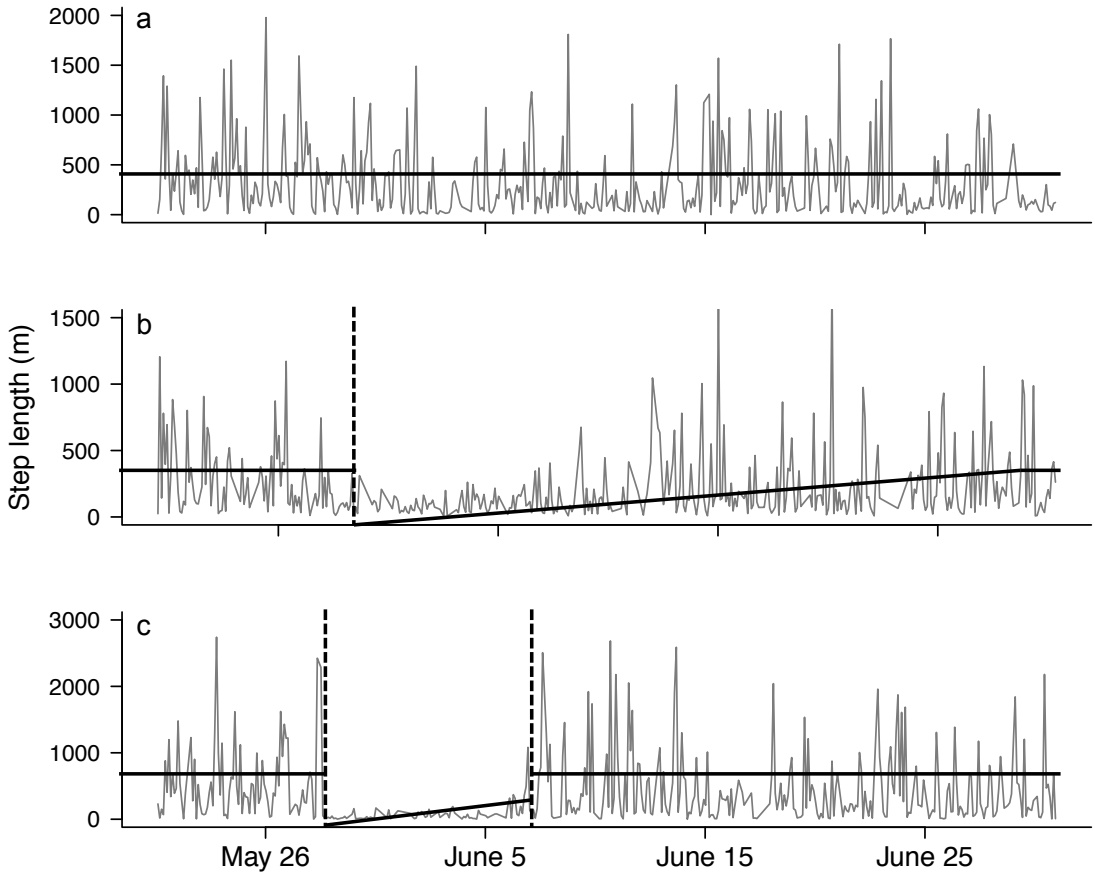

Figure 2.2. Examples of *a priori* movement models used in an individual-based method to infer parturition and calf mortality events in female woodland caribou (*Rangifer tarandus caribou*) (sensu [8]) and actual movement characteristics of female caribou. Gray line indicates the movement pattern of a female caribou with the lowest AIC score. Black line indicates the predicted mean step length from movement model. The individual movement

data used to generate the movement patterns were collected from either Fogo Island herd (a and b) or Middle Ridge herd (c). The models suggest that (a) no parturition event occurred, this is indicated by no break point in the mean movement rate. (b) Parturition event occurred on approximately 29 May and no mortality event occurred (prior to four weeks of age), this is indicated by a single break point in mean movement rate followed by a gradual increase in movement rate until mean movement rate reaches that of pre-parturition (at approximately four weeks post-parturition). (c) Parturition event occurred on approximately 28 May then a calf mortality event occurred on approximately 6 June, this is indicated by two break points in mean movement rate, one at the point of parturition and subsequently when the female lost her calf before four weeks and immediately returns to pre-parturition movement rate.

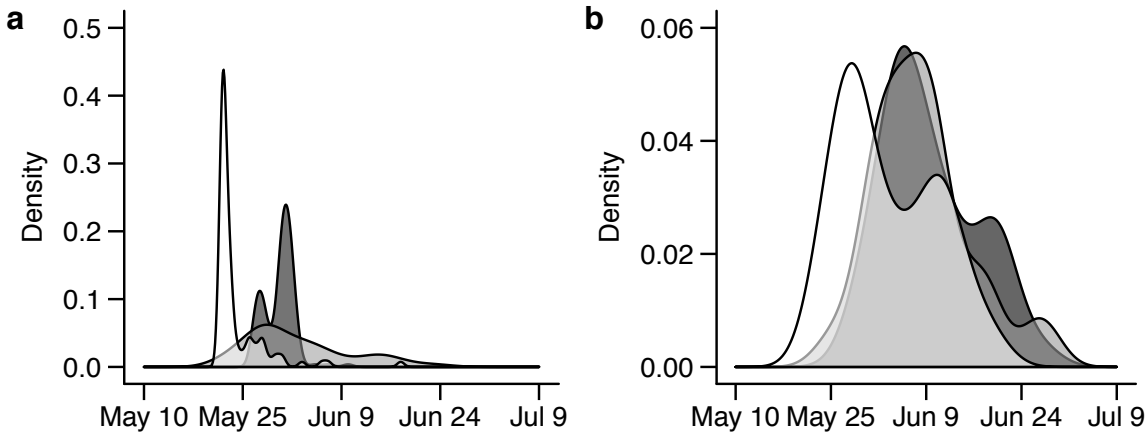

Figure 2.3. Comparison of density distributions of herd-wide VHF calf collaring dates and mortality dates from 134 calves from Middle Ridge herd between 2009–2013 [27] with estimated parturition and calf mortality dates derived from DeMars et al. [8] individual-

based method (IBM) and population-based method (PBM) for 43 adult females from Middle Ridge herd between 2009–2013 (a) Density distributions of herd-wide VHF calf collaring dates (dark gray), estimated parturition dates derived from IBM (light gray) and PBM (no shading). (b) Density distributions of herd-wide VHF calf mortality dates (dark gray), estimated calf mortality dates derived from IBM (light gray) and PBM (no shading).

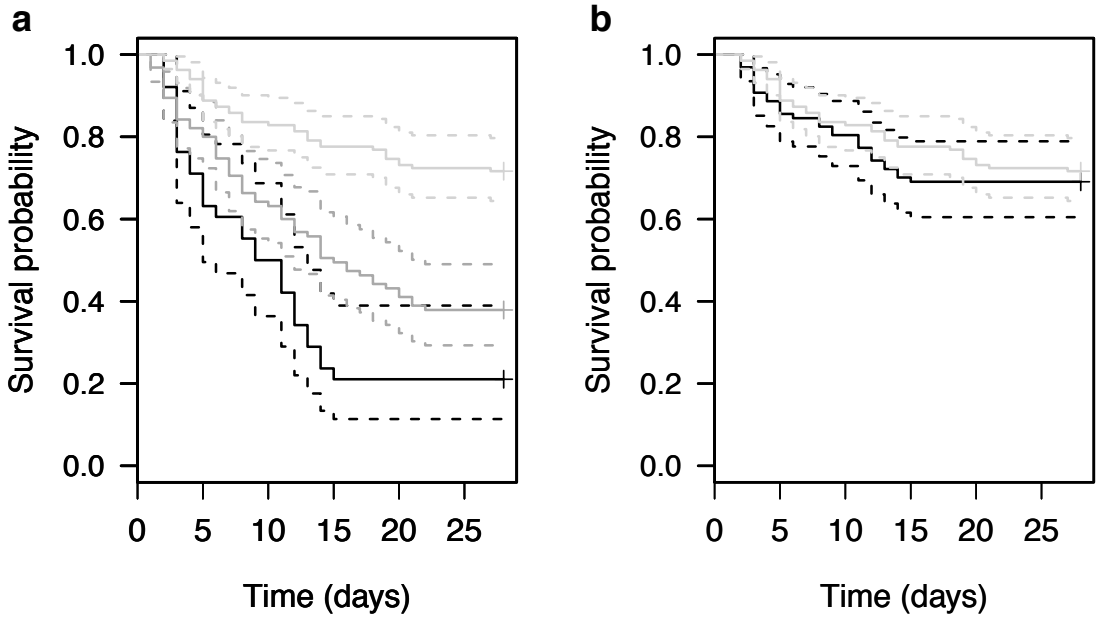

Figure 2.4. (a) Kaplan-Meier survival probability curves comparing survival data generated from 43 GPS-collared females in Middle Ridge from 2009−2013 using DeMars et al.'s [8] individual-based method (IBM; black), and population-based method (PBM; dark gray), and calf mortality from 134 VHF-collared calves in Middle Ridge from 2009−2013 (light gray). Dotted lines are 95% confidence intervals. (b) Kaplan-Meier survival probability curves comparing calf mortality data from 134 VHF-collared calves from Middle Ridge herd from 2009−2013 (light gray) to survival data generated by using a combination of the IBM and PBM models for 43 GPS-collared females in Middle Ridge herd from 2009−2013 (black). Parturition was determined for 43 GPS collared females from 2009–2013 using the

PBM and then calf mortality was determined using the IBM. For calves whose parturition was predicted using the PBM, if the IBM did not predict calf mortality before four weeks I assumed the calf survived.

CHAPTER 3: SEASONAL AGGREGATION IN A GREGARIOUS UNGULATE AND ITS EFFECT ON NEONATE CALF SURVIVAL

3.1 Abstract

Aggregation, the tendency for animals to group together in space, is a phenomenon displayed across a wide range of species. Predation risk is one of the evolutionary forces driving group formation. Two bodies of research hypothesize evolutionary strategies for animal space use during aggregation: the Geometry of the Selfish Herd (GSH) and the Ideal Free Distribution (IFD). The GSH predicts that predation risk and thus fitness vary depending on individual position within the aggregation. However, the dilution-detection trade-off should give rise to two distinct grouping behaviours in response to predation risk: aggregating and disaggregating. The IFD predicts that animals will settle in a manner that equalizes fitness between these two behaviours. Using the combined framework of GSH and IFD, the objective of my research was to explain how aggregation on calving grounds by female caribou influenced calf survival. I predicted that fitness should vary within the aggregation on the calving ground due to the heterogeneous distribution of risk throughout the group according to the GSH hypothesis. However, I predicted that female caribou should distribute themselves on and off the calving ground so that on average fitness should not differ between the two areas, according to the IFD hypothesis. I used telemetry data from n = 43 adult female caribou from 2009–2013 and examined spatially implicit aggregations using pairwise nearest neighbour (NN) distances as a proxy for the degree of aggregation. I found support for the GSH prediction of heterogeneous distribution of fitness not throughout the whole herd, but throughout the group on the calving ground; individuals at the periphery of the social aggregation had a greater chance of calf mortality. I found

support for the IFD prediction that fitness did not vary between strategies; no significant difference in calf mortality between females on and off the calving ground. My work brings together two bodies of research on evolutionary strategies for space use; the results provide empirical support that social cohesion affects fitness.

3.2 Introduction

In social species the choice to aggregate is hypothesized to carry a fitness trade-off. The benefits of aggregating include information transfer about resources (Giraldeau and Caracao 2000), predation dilution and confusion effects (Lehtonen and Jaatinen 2016), facilitating mate choice (Ward and Webster 2016), and physiological benefits such as reduced heat loss (Gilbert et al. 2010). Some disadvantages to aggregating include competition for resources and predator free space (Bateman et al. 2012), increased detection by predators with increased group size, and increase transmission of disease (Vander Wal et al. 2015). More specifically, animals experience an increase in competition for common resources as group size increases that can result in negative fitness consequences and consequently a density-dependent relationship between population size and population growth (Chamaillé-Jammes et al. 2008; Cross et al. 2010; Vander Wal et al. 2013). When benefits outweigh the costs, aggregation behaviour in social species should evolve.

Birthing aggregations, where animals aggregate in large groups shortly before parturition and then give birth in synchrony, are hypothesized to improve an individual's fitness by improving reproductive success. The appearance of a sudden mass of prey is thought to "swamp" a predator's capacity to consume prey and thus reduce the overall number of prey taken from the population (Ims 1990). Classic examples of predator swamping include sea turtle hatching (Santos et al. 2016), and the formation of penguin colonies (Ainley et al. 2005), which show considerable variation in rates of juvenile survival but little variation in adult survival rates. In these scenarios, variation in fitness is directly related to variation in reproductive success. How then might an individual

maximize their fitness in a birthing aggregation? When all individuals are aggregating, might one actually maximize fitness by choosing not to aggregate?

Birthing aggregations represent opportunities for natural selection on social aggregation behaviour. Two bodies of research hypothesize evolutionary strategies for animal space use during aggregation: Geometry of the Selfish Herd and the Ideal Free Distribution. Both frameworks may elucidate how an individual can maximize their reproductive success (and therefore overall fitness) through aggregation behaviour.

3.2.1 The Geometry of the Selfish Herd

The Geometry of the Selfish Herd hypothesis (hereafter GSH) explores how fitness varies with individual spatial position in relation to the rest of the group. Originally proposed by Hamilton (1971) the GSH has been influential in explaining facultative aggregations in response to predation risk. The GSH assumes that an individual's relative predation risk is proportional to their domain of danger (DOD), calculated using Voronoi polygons (Figure 3.1). The area around a given individual that is nearer to them than to any other individual in the group represents their DOD, within which an individual will be closest to a randomly appearing predator. The GSH assumes that a predator can appear from anywhere and when appearing will target the nearest prey. If a predator appears within an individual's DOD, it will successfully attack that individual. Thus, to reduce the risk of predation, individuals should approach their nearest neighbour and reduce the size of their DOD thereby forming tight aggregations. In addition, the GSH predicts that the individuals that are surrounded by others should have the smallest DODs and thus, should have the lowest predation risk. Individuals should therefore seek to position themselves centrally within the group to maximize fitness. Maintaining a central position within the group does indeed come with

costs, such as reduced energy intake if access to food is depleted (Rands et al. 2004). In the case of birthing aggregations, where adult fitness is invariant, and fitness depends on variation in offspring survival, fitness may still be maximized from reduced predation risk despite these costs.

The predictions of the GSH have been supported empirically. Studies have quantified increased cohesiveness within groups when exposed to predators (Viscido 2003), shown that individuals prefer central positions within the group over peripheral positions (Krause and Ruxton 2002; King et al. 2012), and evaluated the behavioural movement that would cause reduction in and individual's DOD (Morrell et al. 2010; Hirsch and Morrell 2011). The critical assumption that the size of the DOD is proportional to predation risk and that predation risk alone accounts for differences in fitness and is thus under selection pressure was empirically tested by De Vos and O'Riain (2010). They found support for this assumption within a population of Cape fur seals (*Arctocephalus pusillus pusillus*).

Following the assumption that predation risk primarily accounts for differences in fitness, I can predict that predation risk, and thus fitness, will be heterogeneously distributed throughout the group. Individuals that are more central to the group will have higher fitness compared to individuals on the periphery. Given the heterogeneous distribution of fitness within the group, in saturated aggregations the fitness of peripheral individuals should reach a point where it is no longer beneficial to aggregate.

3.2.2 The Ideal Free Distribution

The Ideal Free Distribution (hereafter IFD) predicts that individuals should distribute themselves among heterogeneous habitat patches to maximize their fitness (Fretwell and Lucas 1970). The IFD assumes that habitat patches are settled over time, such that the

highest quality patches that provide the greatest fitness benefits are settled first. As high quality patches become saturated, increased competition for resources reduces the potential fitness benefits of the high quality patch to a point where an individual's potential fitness might be the same by moving to a lower quality patch. Settlement in both patches should continue to a point where fitness is equalized across occupied patches (Figure 3.2). The original IFD hypothesis proposed by Fretwell and Lucas (1970) involves three key assumptions. First, IFD assumes that individuals have perfect knowledge of habitat quality and can accurately compare resource availability in all patches and choose the one yielding the highest fitness. Second, IFD assumes that settlement is density-dependent, such that each additional individual reduces the potential fitness gained by all other individuals sharing the patch, thus increasing the relative benefits of lower quality patches that also have lower population density. Finally IFD assumes that density-dependent settlement of patches results in equilibration of fitness, such that individuals no longer need to relocate to maximize their individual fitness. The three core assumptions of IFD are widely used to explain models of habitat partitioning and community diversity (Rosenzweig and Abramsky 1985) as well as in studies of habitat selection (Morris 1989; Morris 2002). Indeed, recent evidence has shown that the IFD represents an evolutionary stable strategy in a two patch scenario (Cressman and Krivan 2006). While the IFD hypothesis can be applied to many study systems, for example Thomsons gazelles (*Eudorcas thomsonii*; Bradbury et al. 2015) and pike (*Esox lucius*; Haugen et al. 2006), other distributions such as ideal despotic distributions may be more applicable in certain systems (Emlen et al. 2003).

The assumptions of the IFD led to the prediction that ideally at equilibrium the proportion of settlers on a patch should match the proportion of resource on that patch. This

has been termed the “input matching rule” or “proportional settlement” (Bradbury et al. 2015). Many laboratory and field experiments show deviations from proportional settlement; too few settlers on richer patches (i.e., undermatching) or too many settlers on richer patches (i.e., overmatching). In these cases, Isodar analysis (Morris 1992) could be used to explore the density-dependent relationship between resource and settlers on a patch, as it does not require proportional settlement (Bradbury et al. 2015).

The IFD hypothesis is often used in studies where a patch is defined based on a resource quality such as forage (Bradbury et al. 2015); however, a patch can also be defined based on the quality of an animal’s social environment (Webber and Vander Wal 2017). In the context of animal aggregations, an individual can choose to aggregate in a group or disaggregate away from the group. The proximate mechanism driving this choice is often predation risk. For gregarious species, an individual's risk of being depredated is typically comprised of the likelihood of one's group being detected and the likelihood of being the one in the group that is attacked. Larger groups are typically easier to detect (Hebblewhite and Pletscher 2002; but see Ioannou et al. 2011; Fryxell 2007), however, an individual’s chance of being attacked decreases evenly with each additional member of the social group (Hamilton 1971). As such, individuals in large groups have a greater likelihood of detection but have a lower per capita risk of being attacked, while a disaggregated individual (e.g., one spaced away from the group) may be less likely to be detected but in the event of an encounter is more likely to be attacked.

Because of the dilution-detection trade-off, I expect two behavioural strategies to persist: disaggregated behaviour (low detection, low dilution) and aggregative behaviour (high detection, high dilution). When I apply the framework of the IFD to a population of

facultatively gregarious individuals, I would predict that individuals would first choose to aggregate and thus receive the fitness benefits associated with group living, i.e., decreased predation risk. However, when the group reaches a certain population density, the costs of group living should outweigh the benefits such that and individual should choose to space away from the group. I would therefore expect that fitness should equalize between aggregate and disaggregated individuals within a population.

3.2.3 The ungulate model: caribou calving aggregations

Many ungulate species choose to aggregate seasonally and give birth in synchrony. Birthing synchrony in ungulates is hypothesized to increase neonatal survival through predator swamping (Bergerud 1975; Estes and Estes 1979). Female ungulates generally trade off foraging opportunities for decreased predation risk (Fryxell 1991) although there is evidence that some ungulates synchronize birthing with seasonal productivity (Festa‐Bianchet 1988; Bowyer et al. 1998). In general for ungulates, adult survival is invariant while juvenile survival varies considerably particularly in the first weeks of life (Gaillard et al. 2000). Thus, contributions to an adult's fitness are largely determined by its reproductive success during this early period post parturition. The degree of aggregation varies seasonally, with female-offspring herds being more tightly aggregated during birthing and when mobility with a calf-at-heel is impaired compared to the rest of the year (Bergerud 1975). Birthing aggregations therefore represent an opportunity for selection (Moorad and Wade 2013) on aggregation behaviour, as variation in both aggregation behaviour and variation in fitness exist. My objective was to empirically test the frameworks of GSH and IFD to elucidate how an individual's aggregation behaviour can

affect fitness in birthing aggregations, using migratory woodland caribou (*Rangifer tarandus*) as a model system.

Caribou calves are highly vulnerable in the first four weeks of life and juvenile mortality is a key factor in determining overall population dynamics (Gaillard et al. 1998; Gaillard et al. 2000). Consequently as a species caribou have developed two spacing strategies to cope with this vulnerability. Sedentary caribou tend to occupy more forested environments and will space away from others during calving to remain inconspicuous (Bergerud 1996). Migratory caribou will usually inhabit open environments and will limit their risk by migrating to above the tree line where they give birth in aggregations on calving grounds. Migration to calving grounds in addition to providing reduce predation risk, may also present increase foraging opportunities (Cameron et al. 1992; Bonenfant et al. 2009).

In Newfoundland, Canada, caribou calves are heavily preyed upon by black bears (*Ursus americanus*) and coyotes (*Canis latrans*) during the first weeks of life (Bastille-Rousseau et al. 2016; Mahoney et al. 2016). Mirroring global caribou declines (Festa-Bianchet et al. 2011) caribou population abundance has declined by more than 60% in the last 10 years in Newfoundland, which led the Committee on the Status of Endangered Wildlife in Canada to designate the caribou populations in Newfoundland as “Special Concern” (Bastille-Rousseau et al. 2013; COSEWIC 2014).

Empirical data has shown that aggregation on calving grounds by female woodland caribou in Newfoundland is predominantly driven by predation risk on juveniles (Bastille-Rousseau et al. 2015; Bastille-Rousseau et al. 2016; Mahoney et al. 2016). Most of the 14 major Newfoundland herds of woodland caribou exhibit some migratory behaviour that

centers on movement to and from calving grounds (Rayl et al. 2014) which is thought to reduce the predation risk facing juveniles during their first weeks of life (Bergerud 1996). Parturient caribou migrate to calving grounds starting in late March or early April and give birth at the end of May. Female-calf herds remain aggregated from June to July after which they disperse (Bergerud 1975). However, the degree of aggregation by females during calving season varies among herds, and can range from highly aggregated to highly dispersed (Rayl et al. 2014). Further, even in highly aggregated herds, there are some females that do not visit the main calving grounds.

If all members of an entire female-calf herd behaved as one single aggregation, then I would predict that the herd would follow the GSH hypothesis where reproductive success should vary depending on degree of aggregation, with individuals in the core of the aggregation having greater reproductive success than individuals on the periphery. However, the dilution-detection trade-off suggests that females arriving at the calving grounds can make the decision to aggregate on the calving ground or disaggregate and remain off the calving ground depending on the fitness benefits conferred by each strategy. Following the IFD hypothesis, I predicted that female caribou will not behave as a single aggregation and should distribute themselves on and off the calving ground so that on average reproductive success should not differ between the two areas. Furthermore, if the herd follows the IFD and does not behave as a single aggregation, I predicted that reproductive success should vary within the aggregation on the calving ground following the GSH hypothesis. Individuals on the periphery of the calving ground should have lower reproductive success compared to individuals in the core of the calving ground.

3.3 Materials and methods

3.3.1 Study Area

I conducted my study in Newfoundland, a 108 860 km^2 island in eastern Canada (47°44 N, 59°28 W to 51°44 N, 52°38 W), with a humid–continental climate and ample year-round precipitation. The landscape consisted of coniferous and mixed forests of balsam fir (*Abies balsamea*), black spruce (*Picea mariana*) and white birch (*Betula papyrifera*), as well as bogs, lakes, and barren rock. My analysis focused on caribou in Middle Ridge herd, located on the south central portion of Newfoundland (for study figure see Appendix D Figure D1).

3.3.2 Caribou telemetry and calf mortality

Adult female caribou were captured using a net gun or darted using the immobilizing agent Carfentanil. Females were captured on wintering grounds from November–January in Middle Ridge North, which is approximately 75 km from the calving grounds in Middle Ridge South. Females were not captured or immobilized during the calving season to avoid transferring immobilizing drugs to calves. GPS 4400M collars (1240g, Lotek Wireless Inc., Newmarket, ON, Canada) were deployed on 43 adult females between 2009 and 2013. A GPS fix was attempted every two hours from May 21–July 31 and every five hours for the remainder of the year. Individual caribou were collared for at least one year, but collars were often re-deployed on the same individuals for up to five years.

I used calf mortality as a proxy for fitness for adult females during calving season. There was no variation in relative adult survival during calving season as none of the 43 collared adult females died over the study period. Since I was only assessing parturient females, I assume that variation in fitness should be solely due to variation in reproductive success. I assessed calf mortality using a movement-based approach (Bonar et al. in review;

Chapter 2) based on the movement rates of GPS collared adult females. Following methods outlined by DeMars et al. (2013) I applied a population-based method that used a moving window approach and evaluated three day average movement rates of adult females to estimate parturition status, and an individual-based method that used maximum likelihood estimation and GPS inter-fix step length of adult females to estimate calf mortality up to four weeks in age. I assume that any detected calf mortalities were due to predation (Bonar et al. in review; Chapter 2).

3.3.3 Social aggregation

Here I am examining the notion that aggregations are a social phenomenon and not necessarily a spatial phenomenon. Therefore, because social cohesion is measured relative to other individuals, the precise geographic locations of the individuals are implicit within the system, but not necessarily specified. I measured pairwise nearest neighbour (NN) distances as an index of the degree of aggregation. I assumed that an individual with large NN distances indicates that individual is disaggregated off the calving ground and an individual with small NN distances indicates that individual is aggregated on the calving ground. Thus the calving ground is not determined in this analysis by an explicit geographic location, and is instead determined based on the degree of aggregation within the herd. Previous studies on Middle Ridge herd have shown that while there is some variation in the range of locations used by female caribou during calving season (i.e., the calving grounds), there was no significant change in the geographic location of the calving grounds between 2009 and 2013 (Rayl et al. 2014). Moreover, empirical evidence suggests that anthropogenic disturbances could result in a reduction in calving site fidelity in adult

female caribou (Faille et al. 2010), making the protection of geographically explicit locations during calving season an ineffective conservation measure.

I made the distinction between individuals residing on and off the calving grounds using NN distances (Stankowich 2003). I ranked individuals according to their seasonal average (May 21–July 15) NN distance and fit the linear model (seasonal average NN distance as a function of ID) with a broken stick regression (Figure 3.3). The inflection point of the regression lines indicated the average NN distance that split the "on" and "off" calving ground groups. Individuals on the calving ground were those fit by the first regression line, and the second regression line in the broken stick regression fit individuals off the calving ground (Figure 3.3; Appendix D Table D1). The inflection points were identified using the "segmented" package (Muggeo 2008) in the program R (R Core Team 2016). I plotted each adult female's centroid point and calculated Voronoi polygons for all individual's for all years using the "voronoi" function in the "dismo" package (Hijmans and Phillips 2017) to visually compare the geographic locations of all individuals with the calving ground delineations made based on the broken stick regression (Figure 3.4). I determined the area of each of the Voronoi polygons and examined the relationship between average NN distance and polygon area for each individual.

3.3.4 Data analysis

3.3.4.1 Geometry of the Selfish Herd analyses

To determine if all individuals followed the predictions of the GSH hypothesis I used a generalized linear mixed model (GLMM) to test for a relationship between NN distance and calf survival to four weeks for all adult females (Chapter 2; Bonar et al. in review) while controlling for year and individual. I used the seasonal average NN distance for each

individual for each year similar to the broken stick regression analysis. I also used a GLMM to test for a relationship between seasonal average NN distance and calf survival for adult females found on the calving ground to determine if individuals aggregated on the calving ground followed the predictions of the GSH hypothesis. Similarly, I used a GLMM to test for a relationship between seasonal average NN distance and calf survival for adult females found off the calving ground however, I did not expect to find a relationship for individuals off the calving ground as disaggregated individuals should not conform to the GSH hypothesis. All GLMM models had a binomial distribution term and a logit link function for the response variable of calf survival, and individual ID and year as random effects.

3.3.4.2 Ideal Free Distribution analyses

To determine whether all individuals followed the predictions of the IFD hypothesis, I used a GLMM to test the effect of calving ground choice (on or off) on calf survival to four weeks while controlling for year and individual. I also examined the proportion of individuals found on and off the calving ground relative to population density to check for proportional settlement between the proportion of individuals found on and off the calving ground. As density increases I would expect to see a constant proportion of individuals off the calving ground if proportional settlement occurs. All GLMMs had a binomial distribution term and a logit link function for the response variable of calf survival, and individual ID and year as random effects.

3.3.4.3 Peripheral and core rarefaction

I wanted to ascertain if there was a NN threshold for individuals aggregated on the calving ground at which animals should consider changing strategies and move off the calving

ground. This threshold would define the core and peripheral groups, with the peripheral group having greater variation in calf loss compared to the core, which would have a lower probability of calf loss overall. I sequentially removed the individual on the calving ground with the largest seasonal average NN distance (i.e., the most peripheral individual) and then re-examined the relationship between calving ground choice on calf survival to four weeks while controlling for year and individual. I continued this sequential rarefaction until there was a significant difference between calf survival on and off the calving ground, or until the sample size was too small to continue.

3.4 Results

Average pairwise NN distances over the entire calving season (May 21- July 15) ranged from 12.43 to 61.61 km (mean = 24.49 ± 9.51 SD) across all years. From the broken stick regressions I determined that 35 out of 43 individuals (82 caribou-years) were found on the calving ground for at least one year and 13 out of 43 individuals (19 caribou-years) were found off the calving ground for at least one year between 2009 and 2013. On average 21 ± 8% (SD) of the collared animals were found off the calving ground each year (range = 13–29%; Figure 3.3). Regression results for all broken stick regressions can be found in Appendix D Table D1.

Over the 101 caribou-years 97 calving events occurred (18 calving events off the calving ground, and 79 calving events on the calving ground). There were 32 calves that were lost before four weeks (7 off the calving ground and 25 on the calving ground), and 64 calves survived to four weeks (11 off the calving ground and 54 on the calving ground).

I found that the calving ground delineations (on/off) based on the broken stick regression matched the geographic locations of each individual when plotted in space

(Figure 3.4). There was a significant linear relationship between average NN distance and area of Voronoi polygons when controlling for year and individual ($t = 6.85$, $p < 0.001$, $R^2 = 0.51$; Figure 3.5). In one case an individual in 2013 was geographically centered within the group on the calving ground but was ranked as being off the calving ground according to the broken stick regression. I therefore changed this individual's category to "on" instead of "off" for all analyses. I ran all analyses with this individual categorized as off the calving ground and overall results did not differ from those presented here (data not shown).

3.4.1 Geometry of the Selfish Herd analyses

I found no significant relationship between calf mortality to four weeks and seasonal average NN distance for all individuals (Figure 3.6a; Table 3.1). This does not support the prediction the entire female-calf herd behaved as one single aggregation and followed the GSH hypothesis.

I found a significant relationship between calf mortality and seasonal average NN distance for individuals on the calving ground where the probability of calf mortality increased with increasing NN distance (Figure 3.6c; Table 3.2). Central individuals had a lower chance of calf loss compared to individuals on the periphery who were >25% more likely to lose their calf (Figure 3.7). No such relationship was found for individuals off the calving ground (Figure 3.6d; Table 3.3). This supports the prediction from the GSH hypothesis for individuals aggregated on the calving ground. Specifically individuals on the periphery of the social aggregation have greater chance of calf mortality.

3.4.2 Ideal Free Distribution analyses

I found no significant difference in calf mortality between individuals on and off the calving ground (Figure 3.6b; Table 3.1). This supports the IFD prediction that fitness does

not vary between strategies (aggregating or disaggregating). I detected a density-dependent relationship in 4 out of the 5 years of data, with the year 2009 having a greater proportion of individuals off the calving ground than would be expected under the IFD hypothesis (Figure 3.8).

3.4.3 Peripheral and core rarefaction

After sequentially removing the individual with the largest NN distance on the calving ground and revaluating the relationship between calf mortality on and off the calving ground I was unable to detect a significant difference, although I detected a near significant difference ($p = 0.052$ for fixed effect) when the maximum NN distance on the calving ground was 17.55 km (Figure 3.7, D2). The sequential removal of individuals also supports the GSH predictions in that it shows that the peripheral individuals are the ones contributing to the variation in fitness.

3.5 Discussion

Birthing aggregations can improve the fitness of individuals by reducing the predation risk of offspring (Ims 1990). Many ungulates aggregate to give birth as an antipredator strategy. Within these birthing aggregations, adult survival is invariant while juvenile survival varies, and thus reproductive success accounts for any fitness differential between individuals (Gaillard et al. 2000). For an individual to maximize their fitness within a birthing aggregation they must maximize the survival of their offspring. The Geometry of the Selfish Herd (GSH) and the Ideal Free Distribution (IFD) hypotheses provide two distinct frameworks that could explain how an individual can maximize their fitness by choosing to aggregate, or choosing to disaggregate during the period where offspring are most vulnerable. I found support for the GSH prediction of heterogeneous distribution of

fitness within the aggregation on the calving ground and I found support for the IFD prediction that fitness did not vary between aggregate and disaggregate individuals.

Remarkably, 4 out of the 5 years showed a density-dependent relationship on and off the calving ground (Figure 3.8). In 2009 there was a greater proportion of individuals found off the calving ground than would be expected for that density according to the IFD hypothesis (Bradbury et al. 2015). This is a much more common finding than proportional settlement is in both laboratory and field experiments, perhaps lending to the decreased enthusiasm for the IFD hypothesis within the behavioural literature (Emlen et al. 2003; Bradbury et al. 2015). A possible explanation for the disproportionate number of individuals found off the calving ground in 2009 is that individuals were responding to additional pressures than predation risk. The average North Atlantic Oscillation index (calculated from December 2008–March 2009; Climate Prediction Centre Internet Team, 2012) was -0.265. This represents a slightly negative phase indicating a colder and drier winter preceding spring 2009. Green-up occurred within the normal range compared to other years (Figure D3). Industrial activity in the area could have caused more individuals to respond to anthropogenic presence. In March 2009 AbitibiBowater, a pulp and paper mill in Grand Falls-Windsor, closed production (Canadian Broadcasting Corporation 2009). Logging for the AbitibiBowater mill occurred in the area surrounding Middle Ridge herd since 1972. It is possible that from May-July of 2009 caribou were still behaving in response to the industrial activity that had been occurring in the area up until February of that year. However, this remains speculation as I lack the data to be able to empirically assess logging impact in the area.

I only sampled a small portion of the individuals in Middle Ridge herd (43 out of approximately 10 000). Consequently I do not know the positions of all remaining uncollared individuals. While my broken stick regression designated individuals with larger NN distances as being off the calving ground, it is possible that these individuals remained in aggregations with uncollared individuals that were proportionally smaller than the larger central aggregation on the calving ground. The plots of the broken stick regressions (Figure 3.3) and the map of spatial locations of individuals (Figure 3.4) show that individuals off the calving ground are not necessarily in groups with each other. This would mean that there would need to be multiple smaller aggregations surrounding the larger aggregation on the calving ground. These smaller groups may still have formed according to density-dependent settlement and would therefore still follow the IFD hypothesis. I would still expect no difference in calf loss between the groups, meaning that my result supporting the IFD hypothesis still holds.

For two behavioural strategies to evolve within a population, a mechanism must exist for the alternatives to have equal fitness (Morris 2011). If the alternative strategy is negatively frequency-dependent, such that with increasing frequency fitness declines relative to that of the primary strategy, then an evolutionary stable frequency may arise where both strategies have equal fitness (Morris 2011). For instance, an explanation for the maintenance of partial migration is a frequency-dependent evolutionary stable state in which the fitness of individuals that migrate and individuals that remain resident are equal (Chapman et al. 2011; Hebblewhite and Merrill 2011). In my study I had a population of both aggregated individuals on the calving ground and individuals that were disaggregated off the calving ground. Because of the trade-off that exists between detection and dilution

(Krause and Ruxton 2002), as the frequency of individuals disaggregating off the calving ground increases, benefits derived from lower chances of detection should decrease thereby increasing the predation risk and reducing the fitness of those individuals choosing that strategy. This frequency-dependent reduction in fitness would be expected to occur relative to individuals on the calving ground. This negative frequency dependence is often seen in producer-scrounger foraging models, when the number of scroungers increases, the number of available food patches decreases consequently due to the decreased numbers of producers thereby increasing the level of competition between individuals (Barnard and Sibly 1981; Giraldeau and Beauchamp 1999). In my study, I found no difference in calf loss between the individuals on and off the calving ground and thus if fitness is equal overall, both behaviours should continue to persist within the population.

In general the GSH and IFD frameworks are separated into two different research silos. Since both hypotheses were originally proposed in the 1970s there has been considerable theoretical and empirical research examining the support for both hypotheses. The GSH hypothesis has received much support in both the laboratory and field experiments. The GSH hypothesis has been highly influential in helping researchers understand the evolution of aggregation behaviour in the context of predation risk (Morton et al. 1994; De Vos and O'Riain 2010). Similarly many tests of the predictions from the IFD hypothesis have been done in both laboratory and field experiments (see Appendix A in Emlen et al. 2003). Particularly in the animal behaviour literature, there has been a decline in the frequency of publications from studies of the IFD as many laboratory and field experiments found undermatching and not proportional settlement between the numbers of individuals settling on high quality patches than would be expected under IFD

predictions (Bradbury et al. 2015). I was able to show here that both frameworks can apply within a single system by finding support for both hypotheses.

In addition, many of the studies failed to meet the assumptions of the IFD hypothesis (e.g., complete knowledge of all habitat patches, or cost free movement between patches; Matsumura et al. 2010). Similarly, it is likely that my study system does not necessarily meet these assumptions. As caribou migrate, they are likely to gain knowledge of the surroundings, and therefore if individuals were moving off the calving ground and back into areas they previously migrated through, we would infer that they meet the assumption of complete knowledge of all patches. However I have no empirical evidence to suggest that when individuals move off the calving ground that they are moving into areas they previously occupied. Furthermore, caribou are highly mobile animals and moving upwards of 20 km off the calving ground would not be especially costly for a caribou, although it may be slightly more costly for a female with a calf-at-heel. Yet, Griffen (2009) argues that the IFD can still be achieved even if assumptions are violated as long as individuals are permitted to move repeatedly between patches until a steady state is reached.

This gives rise to the idea of individuals being able to switch between aggregate and disaggregate behaviours. According to the GSH hypothesis, peripheral individuals would be expected to exhibit switching behaviour, however, core individuals should not exhibit switching behaviours as they confer greater fitness than peripheral individuals. Under the IFD hypothesis, individuals are expected to be completely plastic in their ability to switch between aggregating and disaggregating based on the assumption of cost free movement between patches. An individual should choose to aggregate or disaggregate depending on

the frequency of each strategy exhibited by individuals within their group. A future direction for this work would be to investigate individual level differences in switching behaviour and its relationship with group size and position within the herd. This could be examined within a behavioural reaction norm framework (Dingemanse et al. 2010) and would further elucidate how an individual's social environment influences variation in fitness.

The majority of the IFD literature examines patch quality in terms of the distribution of foraging resources and the trade-off that exist with predation risk, where forage is the determining factor of patch quality. In contrast, my study assumes that patch is a social construct. I assume predation risk and not forage is what determines patch quality as empirical evidence suggests that caribou do not avoid forage-rich habitats that may confer greater predation risk (Bastille-Rousseau et al. 2015). I argue that the GSH and IFD frameworks should not necessarily be considered mutually exclusive when examining aggregation behaviour in ungulates. When aggregation behaviour is to take advantage of the social benefits of aggregation including reduction of predation risk facing offspring, both the GSH and IFD frameworks can apply. While both frameworks can make conflicting predictions in terms of animal space use, in the context of caribou social aggregations I find support for both hypotheses.

3.6 Conclusions and further directions

In this study, I bring together two bodies of research on the evolutionary strategies for space use, Geometry of the Selfish Herd, and the Ideal Free Distribution, and show that both frameworks apply to migratory adult female caribou exhibiting aggregation behaviour and disaggregation behaviour during calving season. I define patch quality as an animal's

social environment as opposed to a geographic environment by using a spatially implicit measure of social cohesion to delineate aggregate and disaggregate behaviour on and off the calving ground. My results provide empirical support that social cohesion affects fitness and that individuals evaluate the costs and benefits of social cohesion following the IFD. My study highlights a number of important avenues for future work including: (1) examining the evolution of space use strategies by measuring the heritability of aggregate and disaggregate behaviour at the individual level, and (2) exploring individual plasticity and repeatability of aggregate and disaggregate behaviours within a behavioural reaction norm framework.

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Table 3.1. Table of values for generalized linear mixed models testing the fixed effect of seasonal average nearest neighbour (NN) distance (model 1) and position on or off the calving ground (model 2) on calf loss for 43 adult female caribou (*Rangifer tarandus*) in Newfoundland, Canada (n = 101 caribou-years). All models had a binomial distribution term and a logit link function for the response variable of calf survival, and individual ID and year as random effects.

Model	Fixed Effects	β Estimate ± SE	t-value	p-value	Random Effects	Variance	Std. Dev.
1	Intercept	-1.27 ± 0.60	-2.11	0.035	ID	0.00	0.00
	Seasonal average NN distance	0.02 ± 0.02	0.90	0.371	Year	0.03	0.17
2	Intercept	-0.52 ± 0.49	-1.06	0.290	ID	0.00	0.00
	Calving ground (On)	-0.31 ± 0.53	-0.54	0.563	Year	0.07	0.26

Table 3.2. Table of values for generalized linear mixed models testing the fixed effect of seasonal average nearest neighbour (NN) distance on calf loss for 35 adult female caribou (*Rangifer tarandus*) in Newfoundland, Canada on the calving ground (n = 82 caribou-years). The model had a binomial distribution term and a logit link function for the response variable of calf survival, and individual ID and year as random effects.

Fixed Effects	β Estimate ± SE	t-value	p-value	Random Effects	Variance	Std. Dev.
Intercept	-1.93 ± 0.42	-4.55	<0.001	ID	0.00	0.00
Seasonal avg NN dist	5.17-05 ± 2.06E-05	2.51	0.01	Year	0.00	0.00

Table 3.3. Table of values for generalized linear mixed models testing the fixed effect of seasonal average nearest neighbour (NN) distance on calf loss for 13 adult female caribou (*Rangifer tarandus*) in Newfoundland, Canada (n = 19 caribou-years) off the calving ground. The model had a binomial distribution term and a logit link function for the response variable of calf survival, and individual ID and year as random effects.

Fixed Effects	β Estimate ± SE	t-value	p-value	Random Effects	Variance	Std. Dev.
Intercept	-5.64E-01 ± 6.00E-01	-0.94	0.347	ID	0.00	0.00
Seasonal avg NN dist	6.47E-07 ± 1.82E-05	0.04	0.972	Year	0.00	0.00

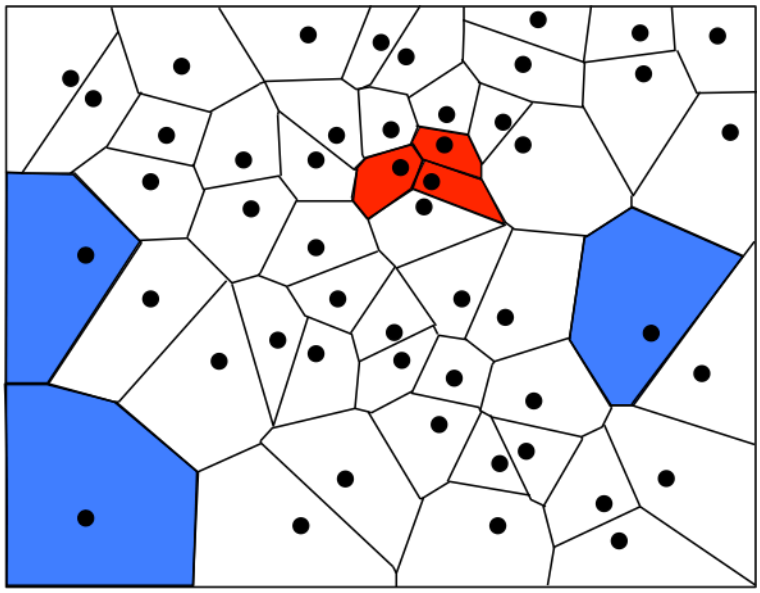

Figure 3.1. The Geometry of the Selfish Herd. A two-dimensional group of animals whose positions are designated by points and the surrounding Voronoi polygons indicate the domain of danger, an area that is nearer to a given individual than to any other individual in the group, within which an individual will be closest to a randomly appearing predator. More central individuals to the group have a smaller domain of danger (red polygons) and thus are at lower risk of predation compared to peripheral individuals that have a larger domain of danger (blue polygons).

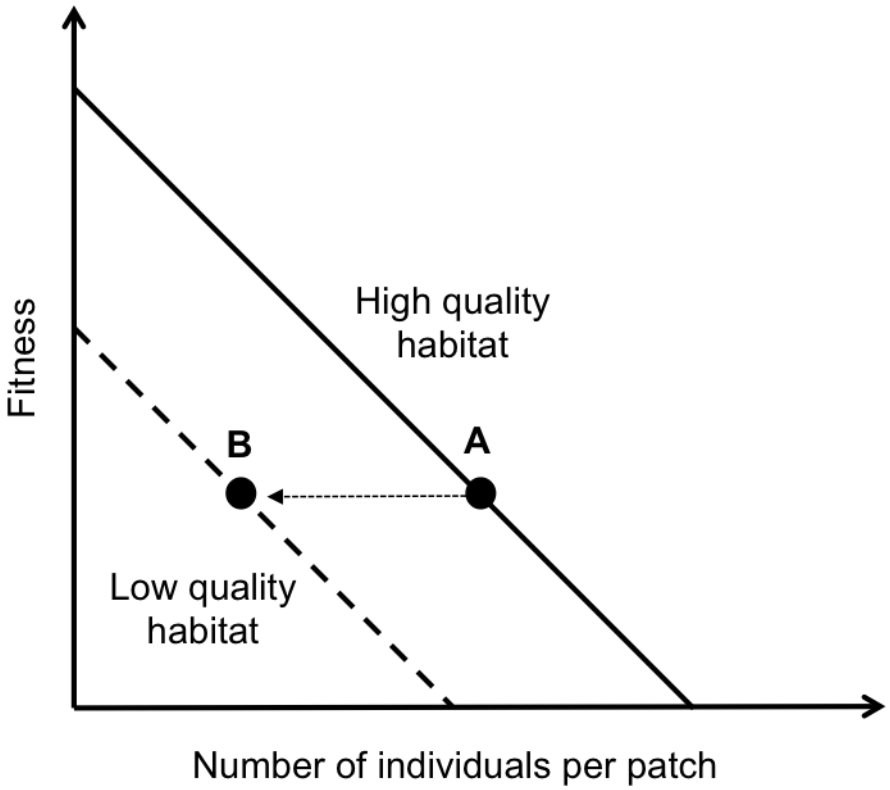

Figure 3.2. The Ideal Free Distribution. Given the existence of high quality (solid line) and low quality (dashed line) habitats, assuming individuals that have complete knowledge of habitat variation should first settle in high quality habitat to maximize fitness. As settlement of high quality habitat continues such that population density increases, increased competition decreases the overall fitness per individual. At some point (point A) it becomes equally beneficial for an individual to move to low quality habitat (point B) and fitness between the two habitats equalizes. Adapted from Ricklefs et al. (7^{th} ed. W. H. Freeman and Co., 2015).

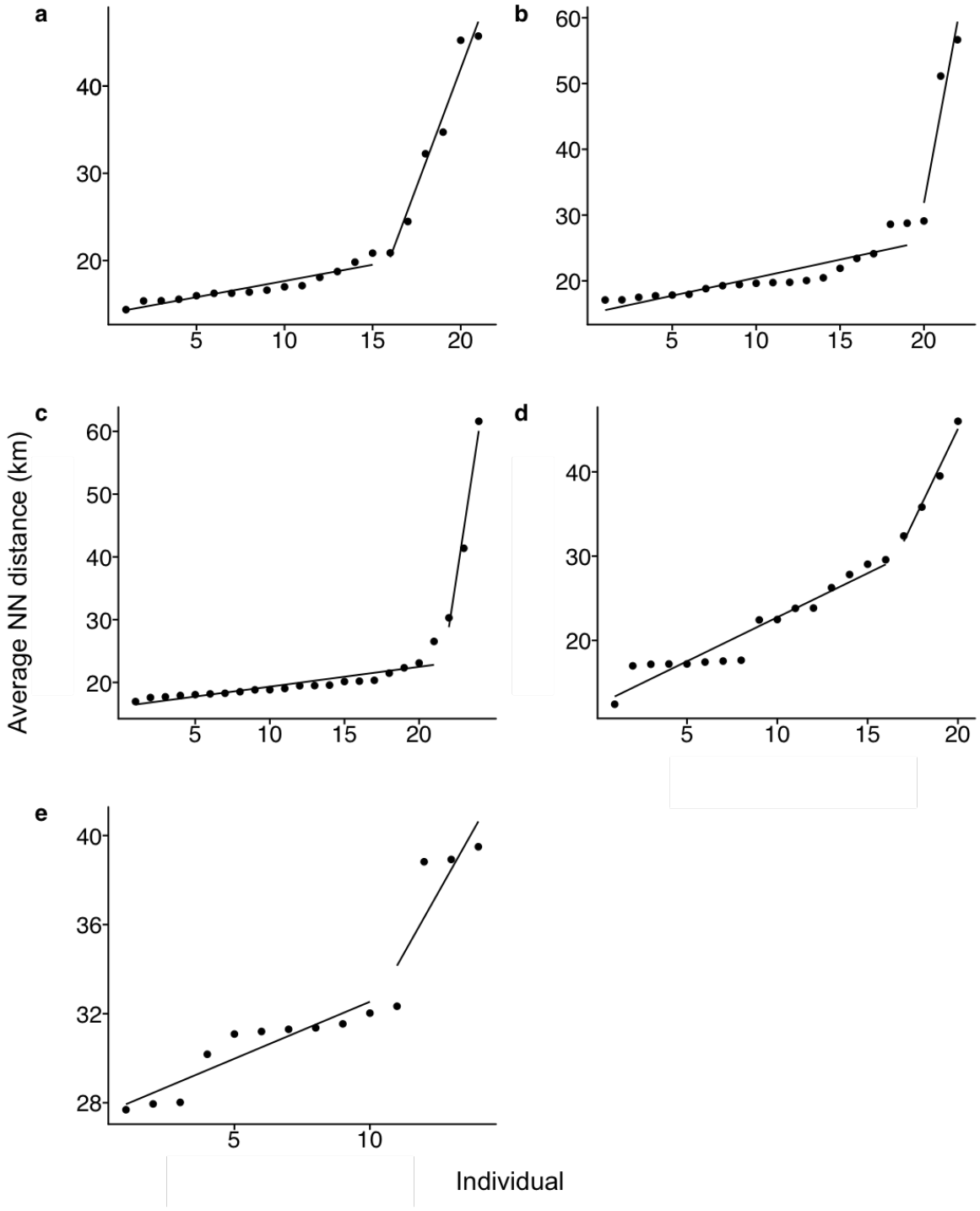

Figure 3.3. Broken stick regressions of ranked seasonal average nearest neighbour (NN) distance for n = 43 adult female caribou (*Rangifer tarandus*) in Newfoundland, Canada (101 caribou-years) from 2009-2013 (a-e respectively). First regression line represents

individuals that were considered to be aggregating while the second line represents individuals who where considered to be disaggregating away from the group.

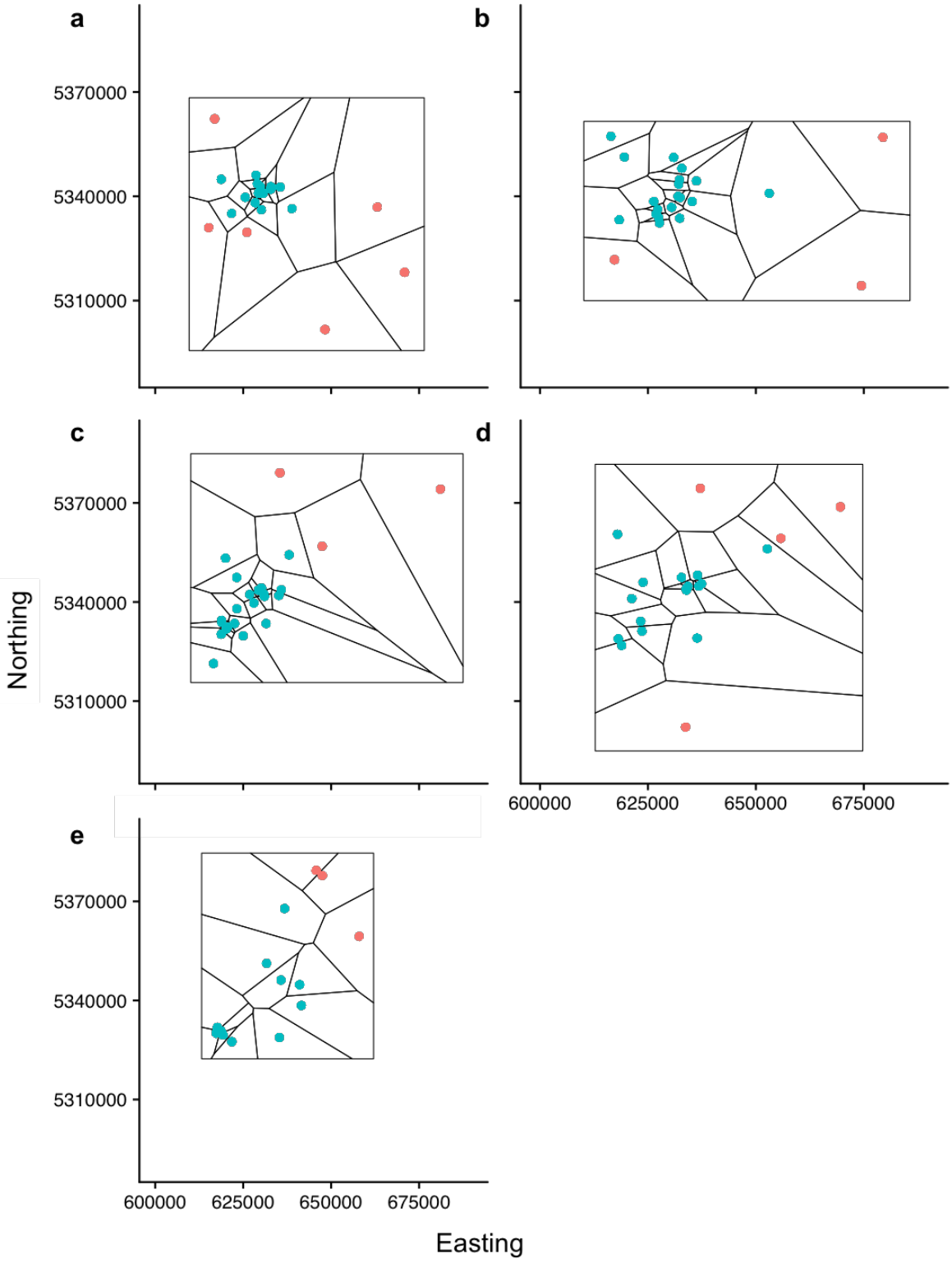
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Figure 3.4. Spatial plots of centroid points for n = 43 adult female caribou (*Rangifer tarandus*) in Newfoundland, Canada (101 caribou-years) from 2009-2013 (a-e respectively). Voronoi polygons surround each individual's centroid and represent an individual's domain of danger, an area that is nearer to a given individual than to any other individual in the group, within which an individual will be closest to a randomly appearing predator. Individuals were designated as on the calving ground (blue) or off the calving ground (red) based on broken stick regressions of average nearest neighbour distance. The extent of the Voronoi polygons is the data range plus 10% (Hijmans and Phillips 2017) but plot extent has remained consistent each year for clarity of scale.

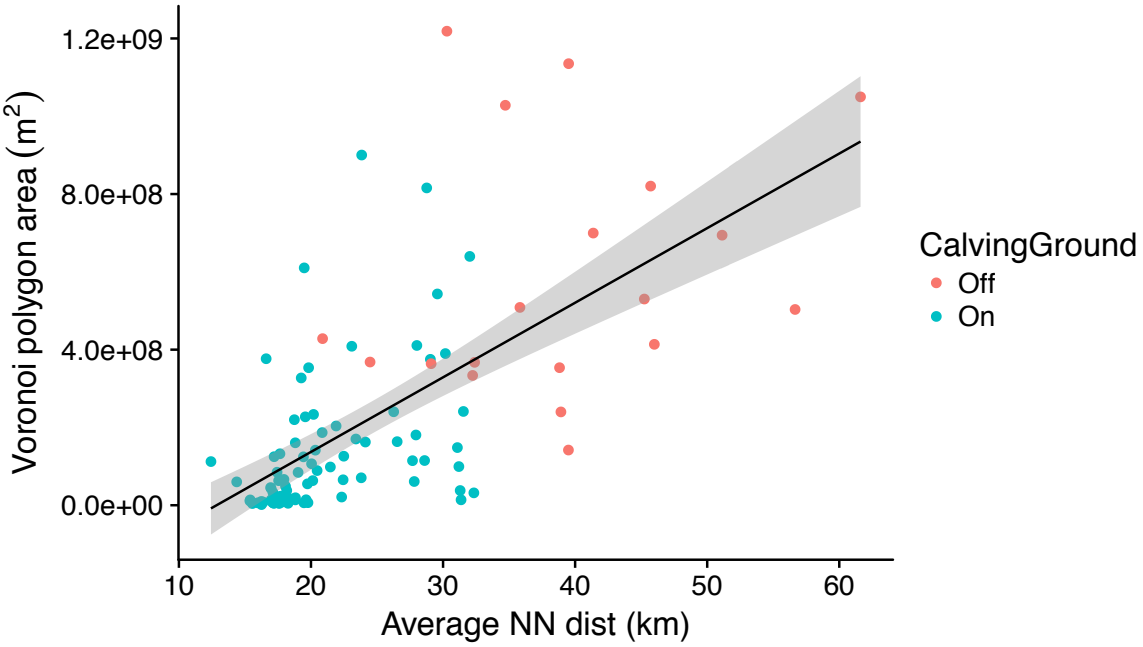

Figure 3.5. Relationship between the average pairwise nearest neighbour (NN) distance and the area of Voronoi polygons (Figure 3.4) surrounding each individual's centroid point for n = 43 adult female caribou (*Rangifer tarandus*) in Newfoundland, Canada (101

caribou-years) from 2009-2013. Individuals were designated as on the calving ground (blue) or off the calving ground (red) based on broken stick regressions of average nearest neighbour distance.

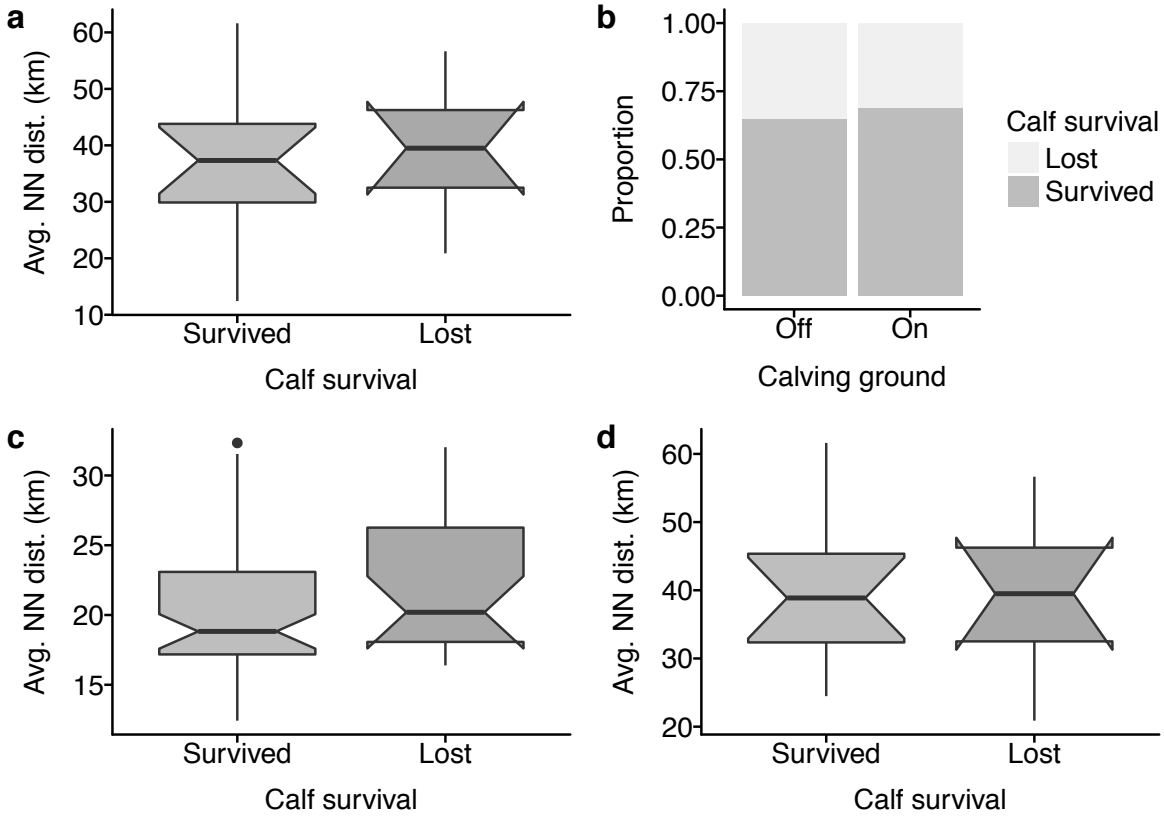

Figure 3.6. (a) Relationship between calf survival and seasonal average nearest neighbour (NN) distance for 43 adult female caribou (*Rangifer tarandus*) in Newfoundland, Canada (n = 101 caribou-years). (b) Proportion of calves that were lost before 4 weeks for 43 adult female caribou on and off the calving ground. (c) Relationship between calf survival and seasonal average NN distance for 35 out of 43 adult female caribou found on the calving ground (n = 81 caribou-years). (d) Relationship between calf survival and seasonal average NN distance for 13 out of 43 adult female caribou found off the calving ground in (n = 20

caribou-years). Data were collected between 2009-2013 and mean pairwise NN distance was averaged over calving season (May 21-July 15).

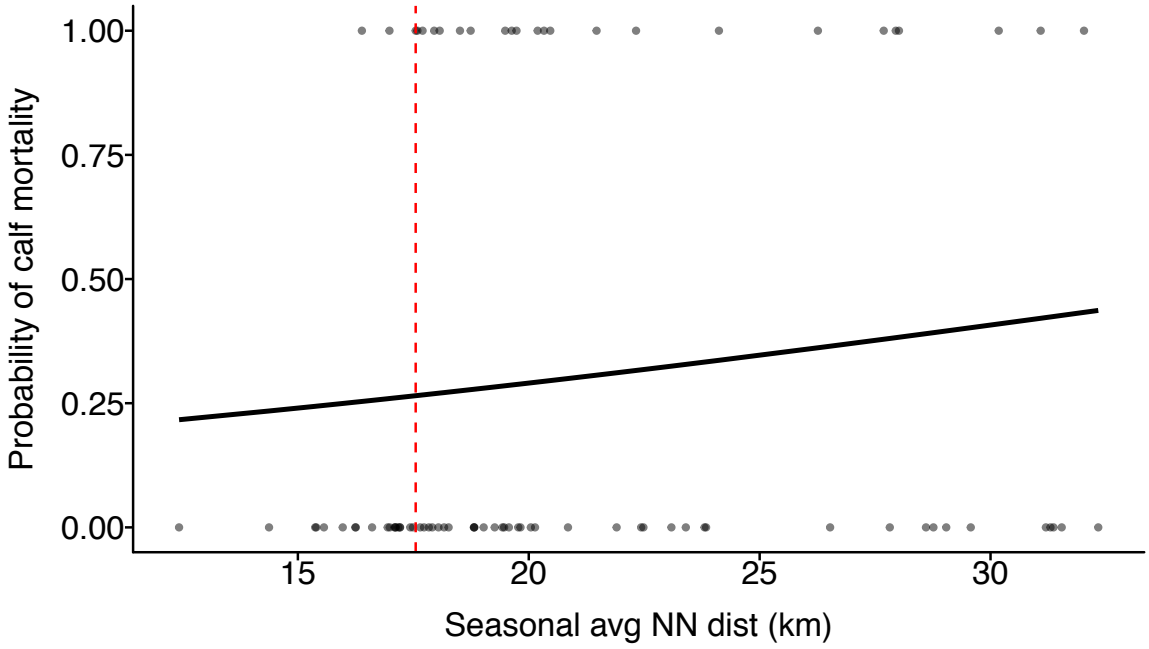

Figure 3.7. Predictive curve from the generalized linear mixed model testing the relationship between calf loss and seasonal average nearest neighbour (NN) distance for 35 out of 43 adult female caribou (*Rangifer tarandus*) that were found on the calving ground in Newfoundland, Canada between 2009-2013 (n = 82 caribou-years). Red line indicates the threshold that delineates the core and peripheral individuals, and individuals above which should consider switching strategies and move off the calving ground. This threshold occurs at 17.55km, which was derived by the sequential removal of peripheral individuals and comparison of calf loss between individuals on and off the calving ground.

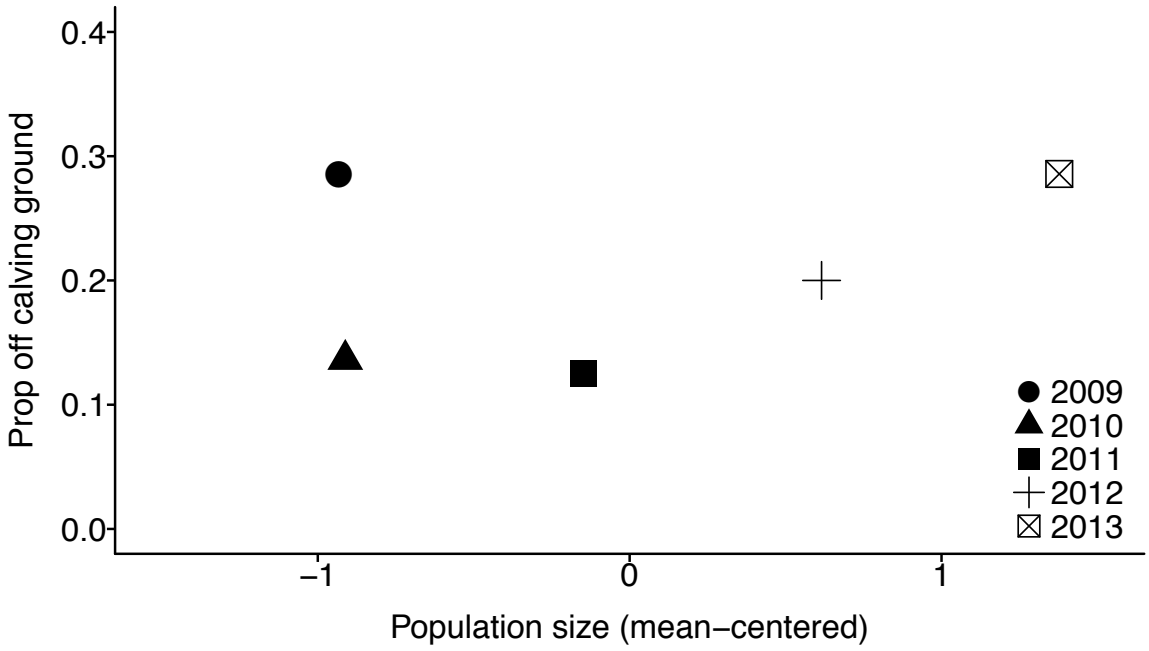

Figure 3.8. Proportion of individuals found off the calving ground as a function of mean-centered population size for 43 adult female caribou (*Rangifer tarandus*) in Newfoundland, Canada between 2009-2013 (n = 101 caribou-years).

CHAPTER 4: SUMMARY AND CONCLUSIONS

4.1 Summary

My research addresses the hypotheses provided by the Geometry of the Selfish Herd (GSH) and the Ideal Free Distribution (IFD) frameworks that could explain how an individual can maximize their fitness by choosing to aggregate or choosing to disaggregate during the period when offspring are most vulnerable (Chapter 3). To estimate fitness metrics I applied two movement-based methods proposed by DeMars et al. (2013) to different ungulate populations and study systems that may violate model assumptions to determine if inferences are possible (Chapter 2). Additionally, I examined the accuracy of these data to generate herd-wide survival estimates and distributions of parturition and calf mortality dates (Chapter 2).

In general, I found the accuracy of both methods was lower for caribou in two herds in Newfoundland relative to what DeMars et al. (2013) observed for caribou in British Columbia. My individual-based model did not preform well at predicting parturition (particularly if calf mortality did not occur), but preformed better at predicting calf mortality. Conversely, my population-based model did not perform well at predicting calf mortality, but predicted parturition with near perfect accuracy. On their own, these methods did not generate accurate herd-wide survival estimates based on VHF-collared calves in Newfoundland. Combined, however, the two methods produced herd-wide survival estimates similar to radio-telemetry. Additionally, I found support for the GSH prediction of heterogeneous distribution of fitness throughout the aggregation on the calving ground. I found support for the IFD prediction that fitness did not vary between aggregate and disaggregate individuals.

4.2 Management implications

Ungulate conservation necessitates an understanding of seasonal aggregation and space use behaviours that ultimately affect individual fitness through offspring survival. While it is important to derive conservation areas based on caribou habitat use patterns, my results indicate that simply protecting areas where large aggregations occur may be insufficient to maximize calf survival (Taillon et al. 2012). Managers should consider that calving away from the calving ground is not necessarily a maladaptive strategy for caribou; areas other than where large calving aggregations occur, could have significant conservation value in terms of improving juvenile survival and the long-term persistence of caribou populations.

In addition to understanding space use, collection of important data on fitness measures, such as parturition and neonate survival, are required to understand population dynamics (Eberhardt 2002). The DeMars model represents an elegant application of movement ecology that may ultimately lead to effective remote quantification of parturition and neonate mortality, thereby adding yet another measure of an important vital rate to a manager's toolbox. With its reliance on only maternal GPS data, the DeMars model allows for a more effective use of scarce financial and human resources by allowing multiple analyses and study objectives to be derived from the same telemetry dataset. However, the limited performance of the model on these data likely presents a problem for the transferability of this model to other ungulate species, other caribou ecotypes, or even caribou populations that exhibit variation in movement behaviour different from those studied by DeMars et al. (2013). By taking a synthetic approach to the models and producing composite reuslts, I was able to overcome the limitations in these data. Thus, if

wildlife managers and researchers have a method for validating the DeMars model within their species and system, the DeMars model may be used to make successful inferences on parturition and calf mortality despite violating its assumptions.

4.3 Future directions

The DeMars model is particularly valuable because it permits retrospective analysis to assess vital statistics (e.g., parturition and calf survival) from GPS telemetry data (DeMars et al. 2013). There are six major herds in Newfoundland that have been extensively monitored using GPS collars since 2006: Buchans, La Poile, Topsail, Grey River, Pot Hill, and Middle Ridge. All six of these herds have experienced population declines over the past fifteen years. There is potential to retrospectively measure reproduction and survival using the DeMars model for the remaining five herds. Individual-based fitness data could be used to make inferences about population dynamics, which is critical should the population decline of Newfoundland caribou continue (Bastille-Rousseau et al. 2016). Additionally, the DeMars model could be extended to make inferences for other ungulate species by adapting the models to include additional movement covariates (e.g., turning angles or net squared displacement) that may explain the movement behaviour of other ungulates.

Additionally, a future direction for this work would be to investigate individual level differences in switching behaviour and its relationship with size of the aggregation and position within the herd. Under the IFD hypothesis, individuals are expected to be completely plastic in their ability to switch between aggregating and disaggregating based on the assumption of cost free movement between patches. An individual should choose to aggregate or disaggregate depending on the frequency of each strategy exhibited by

individuals within their group. According to the GSH hypothesis, peripheral individuals would be expected to exhibit switching behaviour and core individuals should not exhibit switching behaviour as they confer greater fitness then peripheral individuals. Movement and space use behaviours have been linked to variation in personality (Webber et al. in review). Therefore this question could be examined within a behavioural reaction norm framework (Dingemanse et al. 2010) and would further elucidate how an individual's social environment influences variation in fitness. Future studies could examine the repeatability with which an individual chooses to aggregate year-to-year and measure the proportion of the population that tends to switch behaviours. Ultimately, from an evolutionary standpoint, the repeatability of aggregation behaviour would represent the upper limit of the heritability of that behaviour within the population (Dochtermann et al. 2014).

While my work explores the effect of individual variation in post-migration aggregation behaviour on fitness, future work could examine the individual variation in migratory behaviour preceding the arrival at the calving ground and how variation in divergent migratory behaviours influences post-migration aggregation behaviour and ultimately fitness.

4.4 References

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APPENDIX A. CHAPTER 2 SUPPLEMENTARY FIGURES AND TABLES

A.1 Supplementary Tables

Table A1. Akiake's Information Criteria (AIC) generated by the individual-based method from DeMars et al. (2013) for 19 calf-cow pairs from Middle Ridge and Fogo Island herds. The three models compared using the individual-based method are as follows: Model 1 = no parturition; Model 2 = calf survived to four weeks old; and Model 3 = calf mortality occurred before the calf was four weeks old. Change in AIC (ΔAIC) is calculated by taking the difference between the AIC of the model and the model with the smallest AIC value.

ID[1]	AIC Model 1	AIC Model 2	AIC Model 3	ΔAIC Model 1	ΔAIC Model 2	ΔAIC Model 3
MR2009a27	5943.95	5840.10	5808.04	135.91	32.07	0.00
MR2009a25	6035.76	6438.12	6187.19	0.00	402.36	151.43
MR2009a09	6247.69	6513.10	6422.48	0.00	265.40	174.79
MR2009a08	5898.88	6304.09	6113.33	0.00	405.21	214.44
MR2009a16	5967.39	6215.97	6152.40	0.00	248.58	185.01
MR2009a06	6428.29	6368.80	6351.21	77.09	17.59	0.00
MR2009a04	5955.90	6176.01	6135.47	0.00	220.11	179.57
MR2009a07	6085.90	6163.69	6079.07	6.83	84.61	0.00
MR2009a26	5128.08	5039.96	5042.58	88.12	0.00	2.62
MR2009a01	6253.55	6633.27	6509.98	0.00	379.73	256.43

FO2016002	9515.51	9778.49	9705.34	0.00	262.99	189.84
FO2016003	9369.66	9313.94	9312.71	56.95	1.23	0.00
FO2016004	8835.30	8928.34	8919.01	0.00	93.05	83.72
FO2016005	9488.24	9594.58	9544.68	0.00	106.34	56.44
FO2016010	9539.01	9492.50	9494.45	46.50	0.00	1.94
FO2016011	12363.93	12405.96	12402.30	0.00	42.03	38.37
FO2016012	9897.95	9861.59	9809.29	88.66	52.30	0.00
FO2016014	10169.65	10195.96	10183.35	0.00	26.31	13.70
FO2016015	7085.52	7422.94	7402.92	0.00	337.42	317.40

[1]Individual IDs beginning with MR are from Middle Ridge herd and individual IDs beginning with FO are from Fogo Island

Table A2. Parturition and calf mortality predictions generated by the population-based method (PBM) from DeMars et al. (2013) for 19 calf-cow pairs from Middle Ridge and Fogo Island herds. The predictions were generated by iteratively sampling of 5 out of the 9 females that could be used to generate the calving and calf loss thresholds for the model and testing on the remaining 14 individuals for all possible combinations. Predictions were pooled and the proportion of each prediction was calculated for every individual.

	Known Status		**PBM Predictions (proportion of time each status was predicted)**			
ID[1]	**Parturition**	**Calf Survival**	**Parturition**	**No Parturition**	**Calf Mortality**	**Calf Survived**
MR2009a01	Parturition	Survived	1.00	0.00	1.00	0.00

MR2009a04	Parturition	Survived	1.00	0.00	0.00	1.00
MR2009a06	Parturition	Mortality	1.00	0.00	0.50	0.50
MR2009a07	Parturition	Mortality	1.00	0.00	0.50	0.50
MR2009a08	Parturition	Survived	1.00	0.00	0.08	0.92
MR2009a09	Parturition	Survived	1.00	0.00	0.47	0.53
MR2009a16	Parturition	Survived	1.00	0.00	0.07	0.93
MR2009a25	Parturition	Survived	1.00	0.00	0.38	0.63
MR2009a26	Parturition	Survived	1.00	0.00	0.01	0.99
MR2009a27	Parturition	Mortality	1.00	0.00	0.50	0.50
FO2016002	Parturition	Mortality	1.00	0.00	0.44	0.56
FO2016003	Parturition	Survived	1.00	0.00	0.00	1.00
FO2016004	Parturition	Survived	1.00	0.00	0.00	1.00
FO2016005	No Parturition	NA	1.00	0.00	0.05	0.95
FO2016010	Parturition	Mortality	1.00	0.00	0.02	0.98
FO2016011	Parturition	Survived	1.00	0.00	0.00	1.00
FO2016012	Parturition	Mortality	1.00	0.00	0.00	1.00
FO2016014	Parturition	Mortality	1.00	0.00	0.00	1.00
FO2016015	No Parturition	NA	1.00	0.00	1.00	0.00

[1]Individual IDs beginning with MR are from Middle Ridge herd and individual IDs beginning with FO are from Fogo Island herd.

Table A3. Parturition and mortality dates predicted from the individual-based method (IBM) and population-based method (PBM) developed by DeMars et al. (2013) for 43 GPS-collared females in Middle Ridge from 2009−2013. Individuals predicted to have had a parturition event by either or both models are included. Date format is YY-MM-DD.

		IBM		PBM	
ID[1]	**Year**	**Parturition date**	**Mortality date**	**Parturition date**	**Mortality date**
MR2009a01	2009			09-05-22	09-05-29
MR2009a02	2009			09-05-22	09-06-03
MR2009a03	2009	09-06-06	09-06-18	09-05-22	09-05-29
MR2009a04	2009			09-05-22	
MR2009a06	2009	09-05-31	09-06-09	09-05-31	09-06-12
MR2009a07	2009	09-06-02	09-06-05	09-05-22	
MR2009a08	2009			09-05-22	
MR2009a09	2009			09-05-23	09-05-27
MR2009a11	2009			09-05-22	09-06-07
MR2009a13	2009			09-05-22	09-06-06
MR2009a14	2009	09-06-18	09-06-03	09-05-22	
MR2009a15	2009			09-05-22	
MR2009a16	2009			09-05-22	
MR2009a17	2009	09-06-23	09-06-28	09-05-22	09-06-02

MR2009a18	2009			09-05-22	09-05-28
MR2009a21	2009			09-05-23	09-05-30
MR2009a23	2009			09-05-22	
MR2009a24	2009			09-05-22	09-06-13
MR2009a25	2009			09-05-23	
MR2009a26	2009		09-06-28	09-05-22	
MR2009a27	2009	09-05-28	09-06-06	09-05-28	09-06-10
MR2009a02	2010	10-06-02	10-06-17	10-05-24	10-05-27
MR2009a03	2010			10-05-22	10-05-29
MR2009a04	2010			10-05-22	10-05-30
MR2009a06	2010			10-05-22	
MR2009a07	2010	10-05-29	10-06-19	10-05-22	
MR2009a08	2010	10-05-28	10-06-01	10-05-22	10-05-24
MR2009a09	2010		10-06-28	10-05-31	
MR2009a11	2010			10-05-22	
MR2009a14	2010			10-05-22	10-06-05
MR2009a15	2010	10-06-04	10-06-19	10-05-22	10-05-30
MR2009a16	2010			10-05-22	
MR2009a17	2010	10-06-08	10-06-11	10-05-22	10-06-05
MR2009a18	2010			10-05-26	10-05-29
MR2009a21	2010			10-06-18	10-06-20

MR2009a24	2010	10-06-16	10-06-28	10-05-22	10-06-10
MR2009a25	2010	10-06-15	10-06-26	10-05-22	
MR2009a26	2010			10-05-22	
MR2009a27	2010			10-05-22	10-05-28
MR2009a28	2010	10-05-23		10-05-24	10-06-02
MR2009a29	2010			10-05-29	10-06-19
MR2009a30	2010	10-06-03	10-06-11	10-06-03	
MR2009a31	2010	10-05-28	10-06-28	10-05-22	10-05-25
MR2009a02	2011			11-05-30	11-06-13
MR2009a03	2011	11-06-04	11-06-18	11-05-23	
MR2009a06	2011			11-05-22	
MR2009a07	2011	11-05-30	11-06-01	11-05-22	11-05-28
MR2009a08	2011	11-06-01	11-06-06	11-05-22	11-05-30
MR2009a09	2011			11-05-28	11-06-13
MR2009a10	2011			11-05-30	11-06-10
MR2009a11	2011			11-05-22	11-06-03
MR2009a14	2011			11-05-22	
MR2009a16	2011			11-05-22	
MR2009a18	2011			11-05-23	
MR2009a21	2011	11-05-29	11-06-02	11-05-23	11-05-27
MR2009a24	2011			11-05-22	

MR2009a25	2011			11-05-24	
MR2009a27	2011			11-05-22	
MR2009a28	2011			11-05-22	
MR2009a30	2011			11-05-22	11-06-01
MR2009a31	2011	11-05-26	11-06-29	11-05-23	
MR2010a01	2011			11-05-22	
MR2010a03	2011			11-05-22	
MR2011a01	2011	11-06-06	11-06-12	11-06-07	11-06-12
MR2011a02	2011	11-05-28	11-06-10	11-05-28	11-06-15
MR2011a03	2011	11-05-27	11-06-10	11-05-28	11-06-11
MR2011a04	2011	11-05-28	11-06-08	11-05-22	
MR2011a05	2011	11-06-13	11-06-15	11-05-22	11-05-30
MR2011a06	2011			11-05-22	11-05-28
MR2009a02	2012	12-05-29	12-06-01	12-05-24	12-06-10
MR2009a03	2012	12-06-07	12-06-29	12-05-22	
MR2009a06	2012			12-05-22	12-05-23
MR2009a07	2012			12-05-22	
MR2009a08	2012			12-05-22	12-05-24
MR2009a09	2012			12-05-25	12-05-27
MR2009a10	2012	12-05-28	12-05-31	12-05-26	12-06-06
MR2009a18	2012	12-06-04	12-06-09	12-05-27	12-05-29

MR2009a21	2012			12-05-22	12-06-11
MR2009a25	2012			12-05-24	
MR2009a30	2012			12-05-25	12-06-15
MR2009a31	2012			12-05-22	12-05-25
MR2010a01	2012			12-05-22	
MR2011a01	2012	12-06-14	12-06-26	12-06-05	12-06-08
MR2011a02	2012			12-05-22	12-05-24
MR2011a04	2012			12-05-25	
MR2009a03	2013		13-06-26	13-05-22	
MR2009a06	2013			13-05-22	13-05-23
MR2009a09	2013	13-05-23	13-06-05	13-05-22	
MR2009a10	2013			13-05-23	13-06-10
MR2009a25	2013	13-05-23	13-05-25	13-05-23	13-05-28
MR2009a31	2013			13-05-22	13-05-23
MR2011a01	2013	13-06-13	13-06-28	13-05-22	13-05-24
MR2011a04	2013	13-05-24	13-05-29	13-05-22	
MR2012a01	2013	13-05-27	13-06-04	13-05-22	
MR2012a02	2013			13-05-22	
MR2012a03	2013			13-05-26	13-06-04
MR2012a04	2013	13-06-03	13-06-06	13-05-22	13-05-28
MR2012a05	2013	13-05-28	13-05-31	13-05-27	13-06-16

MR2012a06	2013	13-05-29	13-06-09	13-05-27	13-06-10
MR 2013a15	2013	13-05-27	13-06-08	13-05-22	

[1]Individual IDs beginning with MR are from Middle Ridge herd and individual IDs beginning with FO are from Fogo Island herd.

A.2 Supplementary Figures

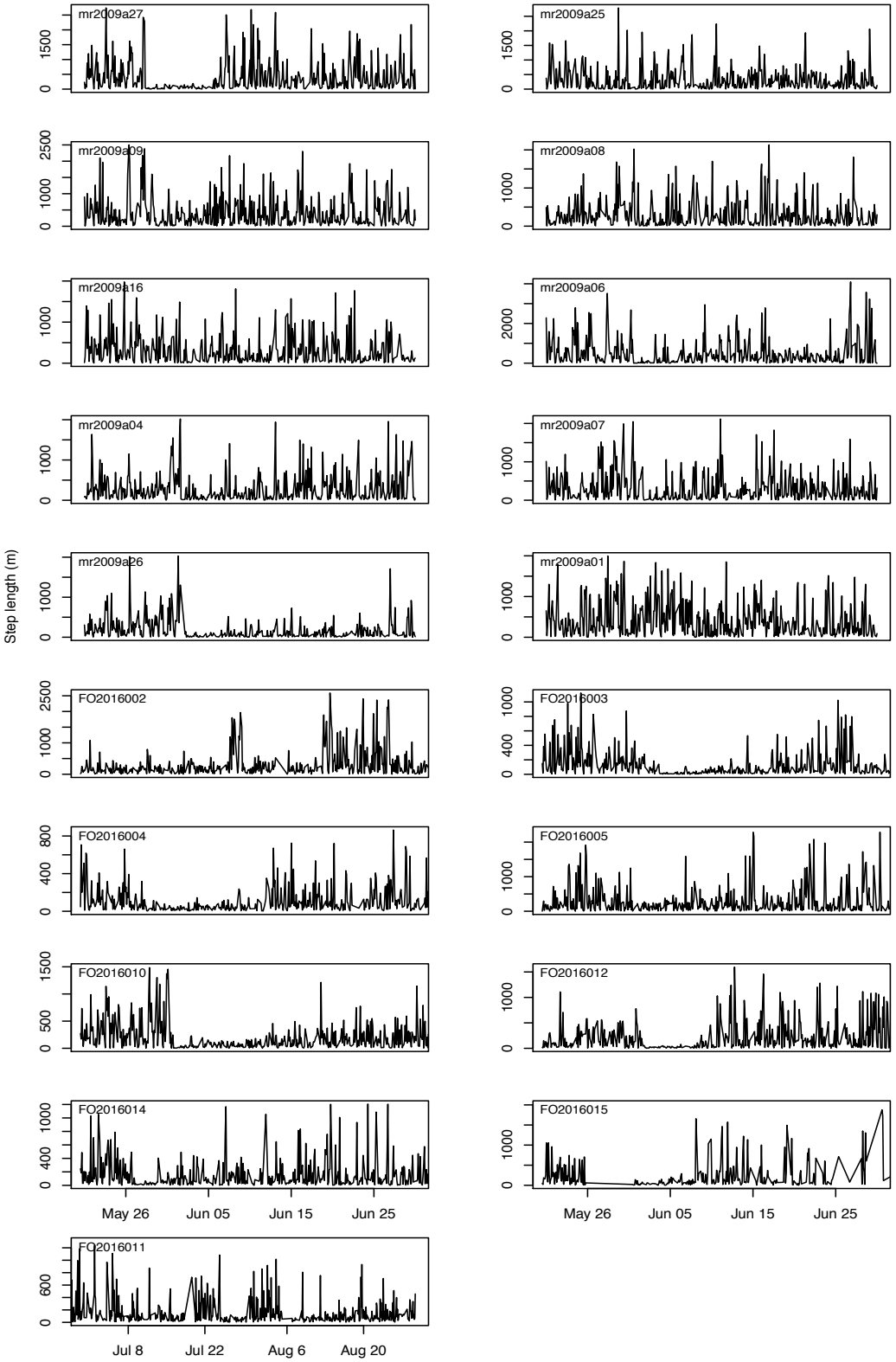

Figure A1. Time-series of step lengths for the 19 calf-cow pairs from Middle Ridge herd and Fogo Island herd. I tested my methods over the time interval 21 May – 30 July for every individual in the Middle Ridge herd and 8 individuals in the Fogo Island herd. I tested my methods over the time interval 30 May – 30 August for one individual to account for a record-late birth in the Fogo herd in 2016 (Bonar et al. 2017).

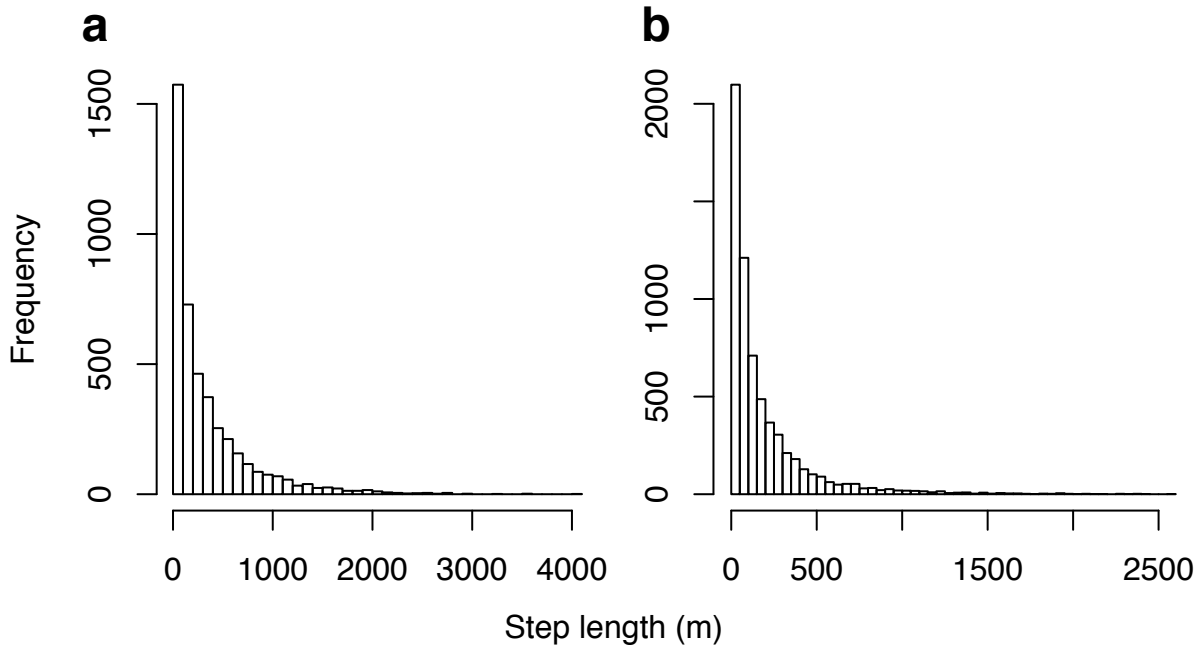

Figure A2. Distribution of step lengths for the 10 calf-cow pairs from Middle Ridge herd (a) and 9 calf-cow pairs from Fogo Island herd (b). Both herds fit the assumption of exponentially distributed step lengths (DeMars et al. 2013).

A.3 References

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APPENDIX B. CHAPTER 2 R CODE FOR POPULATION-BASED METHOD

B.1 R Code for Population-based Method

Following DeMars et al. (2013), my population-based model (PBM) used population level event thresholds (parturition and calf mortality) of 3-day average movement rates (TDAM) in a 3-day moving window analysis to predict calving and calf survival events. To define the parturition threshold, I first generated a distribution of TDAM rates for 3 days post-calving for females who had calves survive to 1 week. I then converted the distribution of movement rates to a kernel density estimate (KDE), which represented the population-level distribution of TDAM rates 3 days post-calving. I transformed this KDE into a cumulative distribution function (CDF) that represented the proportion of the population expected to move at or below this threshold. I then took the 99.9% quantile of the CDF as the parturition threshold; I assumed that movement below this threshold during the moving window analysis indicated calving (DeMars et al. 2013). To more accurately reflect the true 3-day post-parturition window and thus improve the biological accuracy of the parturition threshold, I estimated parturition date as 1 day prior to calf captures.

I followed the same methods to generate the calf mortality threshold from a distribution of TDAM rates, this time for 2-4 weeks post-parturition for females who had calves survive to 4 weeks old. The 99.9% quantile of CDF from this data represented the maximum TDAM rate of a female with a calf up to four weeks old (i.e., calf mortality threshold); I assumed that movement above this rate indicated calf mortality (DeMars et al. 2013).

Prior to calculating the parturition and calf mortality thresholds, I rarefied the data to exclude the top 1% of step lengths. This removed any step lengths that could have been associated with calf capture or predator avoidance (DeMars et al. 2013). I generated the parturition and calf mortality thresholds (in the manner described above) in program R (R Core Team 2016) using a function provided by DeMars et al. (2013). I modified the function used to generate the parturition thresholds to reflect the variation in TDAM rates within my data. This is modification was needed because the range over which I calculated the cumulative distribution function was not large enough with the original code. This is likely due to the wide range of movement rates (17m/hr – 340m/hr) within the dataset used to calculate the event thresholds. I needed to increase the range over which the densityFun is created and thus, changed the line `y <- seq(1, max(rollPool)+20, 0.1)` from `+20` to `+200` to account for the wider range of movement rates.

```
makeThresh <- function(moveRates, timeInt, rare=F, draw=F){
       if (rare==T){
         rarIndex <- apply(moveRates, 2, function(x)
     quantile(x, probs=0.99, na.rm=T))
         for (i in 1:ncol(moveRates)) moveRates[moveRates[,i]
          > rarIndex[i],i] <- NA
       }
       rollAverage <- rollapply(moveRates, 3*24/timeInt,
     mean, na.rm=T, by.column=T)
       rollPool <- as.vector(rollAverage)
       rollDensity <- density(rollPool)
       densityFun <- approxfun(rollDensity$x, rollDensity$y,
     yleft=0, yright=0)
       y <- seq(1, max(rollPool)+20, 0.1)
       rollCumu <- rep(NA, length(y))
       for (i in 1:length(y)) rollCumu[i] <-
     integrate(densityFun, -Inf, y[i], stop.on.error=F)$value
       quant <- 0.999
       threshold <- y[which(rollCumu >= quant)[1]]
       if (draw==T){
```

```
    hist(rollPool, 50, freq=F, xlim=c(0,threshold+10),
  xlab="TDAM mean movement rates", main="Histogram,
  Density and Threshold")
    lines(rollDensity, col='red', lwd=2)
    abline(v=threshold, lwd=2, col='blue')
  }
  return(threshold)
}

makeThreshModified <- function(moveRates, timeInt, rare=F,
draw=F){
  if (rare==T){
  if (rare==T){
    rarIndex <- apply(moveRates, 2, function(x)
  quantile(x, probs=0.99, na.rm=T))
    for (i in 1:ncol(moveRates)) moveRates[moveRates[,i]
     > rarIndex[i],i] <- NA
  }
  rollAverage <- rollapply(moveRates, 3*24/timeInt,
  mean, na.rm=T, by.column=T)
  rollPool <- as.vector(rollAverage)
  rollDensity <- density(rollPool)
  densityFun <- approxfun(rollDensity$x, rollDensity$y,
  yleft=0, yright=0)
  y <- seq(1, max(rollPool)+200, 0.1) # Changed from 20
  to 200
  rollCumu <- rep(NA, length(y))
  for (i in 1:length(y)) rollCumu[i] <-
  integrate(densityFun, -Inf, y[i], stop.on.error=F)$value
  quant <- 0.999
  threshold <- y[which(rollCumu >= quant)[1]]
  if (draw==T){
    hist(rollPool, 50, freq=F, xlim=c(0,threshold+10),
  xlab="TDAM mean movement rates", main="Histogram,
  Density and Threshold")
    lines(rollDensity, col='red', lwd=2)
    abline(v=threshold, lwd=2, col='blue')
  }
  return(threshold)
}
```

B.2 References

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APPENDIX C. CHAPTER 2 4-HOUR GPS INTERVAL DATA

C.1 Estimating parturition and calf mortality events

C.1.1 DeMars individual-based method

Following DeMars et al. (2013), my individual-based model (IBM) for parturition and calf mortality events used three *a priori* models representing the three possible states of a female ungulate during calving season: 1) no parturition; 2) calf survived to four weeks old; and 3) calf mortality occurred before the calf was four weeks old (Figure 2.1). In the model, "no parturition", the mean step length remained constant over time. In the other two models, an event (i.e., parturition or calf mortality) was represented by an abrupt change in the mean step length: a decrease in mean step length represented parturition and an increase represented calf mortality. Thus, in the model, "calf survived to four weeks old", mean step length dropped abruptly, creating a breakpoint at calving, followed by an increase in mean step length with a slope equal to the ratio between the scale parameter and the number of step lengths required for the calf to reach adult movement rates. Conversely, in the model, "calf mortality occurred before four weeks old", mean step length dropped abruptly, creating a break point at parturition, followed by an increase in mean step length with a slope equal to the ratio between the scale parameter and the number of step lengths required for the calf to reach adult rates of movement. This slope, however, was interrupted by an abrupt increase in mean step length to the original mean step length of the adult female at the point of calf mortality (DeMars et al. 2013). All three of the *a priori* models assumed that step length was exponentially distributed and should differ only in the scale parameter (i.e., mean step length).

I rarefied the datasets to exclude the top 1% of step lengths for each individual, which are thought to be associated with calf capture or predator avoidance behaviour (DeMars et al. 2013). I then generated the IBM for the 10 adult females with known calf status from the MR herd in 2009 and the 9 adult females with known calf status from the Fogo herd in 2016. I present graphical representation of step lengths for all 19 adult females with known calf status in Figure C1. After rarefication, the mean per-collar fix rate (number of successful fixes per number of attempts; Frair et al., 2010) was 83% (range: 47-92%). MR appeared to have a higher mean per-collar fix rate (89%, range: 81-92%) than Fogo (76%, range: 47-85%). Following DeMars et al. (2013), I used only step lengths calculated from successive GPS fixes. I used a visual examination of the distributions of step lengths for all 19 calf-cow pairs to determine that the step lengths were exponentially distributed (Figure C2). I then fit the data to each *a priori* model and determined the most supported model using Akaike's Information Criterion (AIC; Burnham and Anderson, 2002). I tested my IBM over the time interval 21 May – 30 July for every individual in the MR herd and 8 individuals in the Fogo herd. I tested my IBM over the time interval 30 May – 30 August for one individual to account for a record-late birth in the Fogo herd in 2016 (Bonar et al. 2017). After applying the IBM to my data, I then compared the predicted calf survival outcomes generated from the IBM with the known outcomes for each female.

C.1.2 DeMars population-based method

The population-based method (PBM) used population level event thresholds (parturition and calf mortality) of 3-day average movement rates (TDAM) in a 3-day moving window analysis to predict calving and calf survival events. Following DeMars et al. (2013), to define the parturition threshold, I first generated a distribution of TDAM rates for 3 days

post-calving for females who had calves survive to 1 week. I then converted the distribution of movement rates to a kernel density estimate (KDE), which represented the population-level distribution of TDAM rates 3 days post-calving. I transformed this KDE into a cumulative distribution function (CDF) that represented the proportion of the population expected to move at or below this threshold. I then took the 99.9% quantile of the CDF as the parturition threshold; I assumed that movement below this threshold during the moving window analysis indicated calving (DeMars et al. 2013). To more accurately reflect the true 3-day post-parturition window and thus improve the biological accuracy of the parturition threshold, I estimated parturition date as 1 day prior to calf captures.

I followed the same methods to generate the calf mortality threshold from a distribution of TDAM rates, this time for 2-4 weeks post-parturition for females who had calves survive to 4 weeks old. The 99.9% quantile of CDF from this data represented the maximum TDAM rate of a female with a calf up to four weeks old (i.e., calf mortality threshold); I assumed that movement above this rate indicated calf mortality (DeMars et al. 2013).

Prior to calculating the parturition and calf mortality thresholds, I rarefied the data to exclude the top 1% of step lengths. This removed any step lengths that could have been associated with calf capture or predator avoidance (DeMars et al. 2013). I generated the parturition and calf mortality thresholds (in the manner described above) in program R (R Coare Team 2016) using a function provided by DeMars et al. (2013). I modified the function used to generate the parturition thresholds to reflect the variation in TDAM rates within my data (Appendix B).

I generated PBM estimates for each herd (MR, Fogo) and the combined herds using the 19 adult females with known parturition and calf mortality events. PBM requires a subset of the population that have experienced both parturition but not calf mortality to generate event thresholds – there was 9 adult females that fit this description (7 in MR and 3 in Fogo). To introduce stochasticity and prevent sampling bias, I iteratively sampled all possible combinations of 5 from the 9 adult females across both herds (n = 126) and all possible combinations of 4 from the 7 adult females in MR (n = 35; i.e., k-fold) for generating event thresholds. The iterative sampling technique was not possible for the Fogo herd as only 3 of the 9 collared females could be used to calculate the calving and calf loss thresholds. This included the female with the record-late birth outside of the calving season (Bonar et al. 2017), which I chose to exclude since the female may not be representative of the whole herd. Therefore, I had only one estimate of event thresholds for the Fogo herd generated using 2 out of 9 collared females. Using these event thresholds, I then compared the PBM-based predictions of parturition and calf mortality events to the known status of all 19 adult females across both herds and for the MR and Fogo herds separately.

C.2 Estimating herd-wide survival, parturition, and mortality date distributions

To generate herd-wide estimates of survival and distributions of parturition and calf mortality dates, I applied both the DeMars IBM and PBM to the 43 GPS-collared adult females from MR. I generated event thresholds using the 7 adult females from the MR herd that had experienced both parturition and calf mortality events. I generated density distributions of the estimated parturition dates and mortality dates from the IBM and the PBM. I also converted the estimated calf parturition and mortality events from the IBM and PBM into Kaplan-Meier survival probability curves using the survival package (Therneau

2015) in R. Following Ellington et al. (in review), I generated herd-wide survival curves and parturition and mortality date distributions from the 134 VHF-collared calves from the MR herd and compared them to survival curve and distributions generated using the DeMars IBM and the PBM. In all analyses, I generated IBM and PBM models using both a 2-hour GPS fix time interval dataset and a rarified 4-hour GPS fix time interval dataset (to mimic the methods used by DeMars et al. 2013).

C.3 Results

Here I present the 4-hour time interval here and I have chosen to present the overall results in the body of the thesis based on the 2-hour time series.

C.3.1 Estimating parturition and calf mortality events

C.3.1.1 DeMars individual-based method

The DeMars IBM failed to definitively distinguish a parturition and calf mortality status for 3 out of 9 adult females from the Fogo herd (in both cases, the models "calf survived to four weeks old" and "calf mortality occurred before calf was four weeks old" were competing. In one case, parturition occurred, and there was no mortality before four weeks (ΔAIC = 1.22), and in the other two cases parturition occurred and calf mortality occurred before four weeks (ΔAIC = 1.99 and ΔAIC = 1.68). Thus in these cases I considered the IBM method successful in predicting parturition but inconclusive in predicting mortality events. The DeMars IBM definitively distinguished (though not always correctly) a parturition event from a calf mortality event for all 10 adult females from the MR herd. AIC and ΔAIC values for all 19 individuals can be found in Table C1.

The IBM correctly classified the two adult females who had no parturition event. The IBM also correctly predicted parturition in 5 of 17 adult female caribou in which parturition occurred (3 of 10 for MR and 5 of 7 for Fogo; Table C2). In situations in which parturition occurred but the IBM method failed to predict parturition (n = 9), calf mortality did not occur in 7 of 9 cases (6 of 7 in MR and 1 of 2 in Fogo; Table C2). Indeed, the IBM method correctly identified only 1 of 10 adult females in which parturition occurred but calf mortality did not occur (1 of 7 in MR and 0 of 3 in Fogo; Table C2). The IBM method predicted calf mortality in 3 of 7 adult female caribou in which calf mortality occurred (2 of 3 for MR and 1 of 4 for Fogo; Table C2).

C.3.1.2 DeMars population-based method

The event thresholds using the PBM were higher in the MR herd than the Fogo herd (parturition: 175 m/hr [range: 117 - 233 m/hr] vs 16 m/hr and calf mortality: 439 m/hr [range: 205 - 585 m/hr] vs 104.1 m/hr). Perhaps this is not surprising given that the dimensions of the island confine space use patterns of caribou in the Fogo herd. The event thresholds using the combined MR and Fogo data were similar to the MR event thresholds, (parturition: 198 m/hr [range: 125 - 257 m/hr] and calf mortality: 426 m/hr [range: 201 - 581 m/hr]).

In general, the PBM performed better for each herd when it used herd-specific event thresholds and when it used event thresholds derived from the combined herds (Table C3), thus I focus my results on PBM based on herd-specific event thresholds. Because of the iterative process in generating event thresholds for the MR herd, the resulting estimates for each event (parturition, no parturition, calf mortality, calf survival) were pooled as proportion of occurrence across all the event thresholds. I considered the prediction

conclusive when the proportion of occurrence was ≥ 0.8 otherwise the prediction was inconclusive. Due to small sample size, there was no iterative process in generating event thresholds for the Fogo herd, thus there were no inconclusive predictions.

The PBM correctly predicted parturition for 16 of 17 females across both herds (for one female in the Fogo herd it predicted parturition when parturition did not occur; Table C4). The PBM did not predict calf mortality correctly and conclusively; in cases where calf mortality occurred the PBM predicted no calf mortality for 3 out of 4 individuals in the Fogo herd (Table C4) and was inconclusive for 2 out of 3 individuals in the MR herd (Table C4). The PBM predicted calf mortality did not occur in 6 of 8 females where calf mortality did not occur (5 of 7 in MR and 1 of 1 in Fogo; Table C4). These results suggested that PBM was more accurate at predicting parturition and the lack of calf mortality than predicting calf mortality, which is opposite to the performance of IBM; the latter was more accurate when predicting parturition with calf mortality than predicting parturition without calf mortality.

C.3.2 Herd-wide survival estimates and distributions of parturition and mortality dates

The predicted distributions of parturition date from the IBM and PBM were different from each other and from the distribution derived from the VHF-collared calves. The IBM predicted that parturition occurred in a wide distribution with only a small peak occurring > 1 week before the observed peak from the VHF-collared calf data, which suggested a long, diffuse calving season (Figure C3a). Conversely, the PBM predicted that parturition occurred in a distribution with a steep peak > 2 weeks before the observed peak from the VHF-collared calf data, which suggested a calving season broadly similar to the observed

calving season but with the majority of parturition events occurring much earlier than they have been observed (Figure C3a). Among individuals with known parturition events, the IBM predicted parturition dates were within 1 day of the collared date (n = 3; i.e., the IBM method when accurate was highly precise; Table C5). The PBM method was highly accurate but predicted parturition dates were typically ≥ 6 days underestimated compared to collar date (n = 8; i.e., the PBM method was highly accurate but had a consistent bias; Table C4)

The predicted distribution of calf mortality dates from the IBM and PBM were broadly similar to the observed distribution from the subset of VHF-collared calves in which mortality occurred prior to 4 weeks of age (Figure C3). The only major discrepancy was that the peak in mortality date occurred slightly later using the PBM than the IBM or the observed VHF-collared calves (Figure C3b). Among individuals with known mortality events (n = 3), the IBM method identified all mortality events but predicted mortality dates varied (-3 to 9 days difference from actual mortality event; i.e., the IBM method was highly accurate but imprecise). The PBM method identified only two of the three known mortality events and consistently overestimated the mortality date (i.e., the PBM method was less accurate and also had a consistent bias).

Both the DeMars IBM and the PBM estimated lower herd-wide survival than what was observed from VHF-collared calves (log-ranked test: $\chi^2 = 17.8$, df = 2, $p < 0.01$; S2 Figure C4a). The IBM estimated 36 parturition events and 25 mortality events, and the PBM estimated 95 parturition events and 4 mortality events. Out of the 134 VHF-collared calves there were 38 mortality events. However, given the performance of the IBM and

PBM when estimating parturition and calf mortality, I generated a survival curve where the PBM was used to identify parturition and the IBM was used to identify mortality (assuming the parturition status identified by PBM). This combined method estimated 104 parturition events and 25 mortality events. Survival rates that I estimated with this combined IBM and PBM method were not statistically different from the 134 VHF collared calves in MR from 2009–2013 (log-ranked test: $\chi^2 = 3.8$, df = 1, p = 0.05; S2 Figure C4b).

C.4 References

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Table C1. Akiake's Information Criteria (AIC) generated by the individual-based method from DeMars et al. (2013) for 19 calf-cow pairs from Middle Ridge and Fogo Island herds for the 4-hour GPS fix interval. The three models compared using the individual-based method are as follows: Model 1 = no parturition; Model 2 = calf survived to four weeks old; and Model 3 = calf mortality occurred before the calf was four weeks old. Change in AIC (ΔAIC) is calculated by taking the difference between the AIC of the model and the model with the smallest AIC value.

ID[1]	AIC Model 1	AIC Model 2	AIC Model 3	ΔAIC Model 1	ΔAIC Model 2	ΔAIC Model 3
MR2009a27	3135.07	3067.55	3047.06	88.01	20.49	0.00
MR2009a25	3263.07	3437.87	3416.38	0.00	174.80	153.31
MR2009a09	3369.87	3507.78	3464.50	0.00	137.91	94.63
MR2009a08	3092.45	3264.64	3207.40	0.00	172.19	114.95
MR2009a16	3143.40	3311.68	3273.03	0.00	168.28	129.62
MR2009a06	3488.31	3449.62	3443.67	44.64	5.96	0.00
MR2009a04	3210.05	3292.67	3286.58	0.00	82.62	76.53
MR2009a07	3279.40	3306.84	3287.95	0.00	27.44	8.55
MR2009a26	2719.00	2687.79	2695.03	31.21	0.00	7.24
MR2009a01	3407.25	3543.85	3581.49	0.00	136.61	174.25
FO2016002	5012.83	5053.01	5042.85	0.00	40.18	30.02
FO2016003	4879.55	4840.27	4841.49	39.28	0.00	1.22

FO2016005	5076.63	5108.17	5093.96	0.00	31.54	17.33
FO2016010	5071.95	4999.64	5001.63	72.31	0.00	1.99
FO2016011	6421.80	6439.54	6440.92	0.00	17.74	19.11
FO2016012	5365.91	5322.87	5306.40	59.51	16.47	0.00
FO2016014	5531.11	5513.53	5515.21	17.58	0.00	1.68
FO2016015	3802.40	3987.18	3977.78	0.00	184.77	175.38

[1]Individual IDs beginning with MR are from Middle Ridge herd and individual IDs beginning with FO are from Fogo Island

Table C2. Parturition and calf status predictions derived from the individual-based method (IBM) from DeMars et al. (2013) for the 4-hour GPS fix interval. Predictions are for 19 calf-cow pairs from Middle Ridge and Fogo Island herd or which calf status was known.

Herd	Status	Observed	IBM Predicted
Middle Ridge	Parturition	10	3
	No Parturition	0	7
	Calf Survival	7	1
	Calf Mortality	3	2
	No Decision	0	0
Fogo Island[1]	Parturition	7	5
	No Parturition	2	4
	Calf Survival	3	0
	Calf Mortality	4	2
	No Decision	0	3

[1] The individual based method for predicting parturition and calf mortality status was inconclusive (competing models) for three adult females

Table C3. Parturition and calf status predictions predicted by the population-based method (PBM) from DeMars et al. (2013) for the 4-hour GPS fix interval for 19 calf-cow pairs from Middle Ridge and Fogo Island herds. The predictions were generated by iteratively sampling of 5 out of the 9 females that could be used to generate the calving and calf loss thresholds for the model and testing on the remaining 14 individuals for all possible combinations. Predictions were pooled and the proportion of each prediction was calculated for every individual.

	Known Status		**PBM Predictions (proportion of time each status was predicted)**			
ID[1]	**Parturition**	**Calf Survival[2]**	**Parturition**	**No Parturition**	**Calf Mortality**	**Calf Survived**
MR2009a01	Parturition	Survived	1.00	0.00	1.00	0.00
MR2009a04	Parturition	Survived	1.00	0.00	0.11	0.89
MR2009a06	Parturition	Mortality	1.00	0.00	0.46	0.54
MR2009a07	Parturition	Mortality	1.00	0.00	0.17	0.83
MR2009a08	Parturition	Survived	1.00	0.00	0.11	0.89
MR2009a09	Parturition	Survived	1.00	0.00	0.38	0.63
MR2009a16	Parturition	Survived	1.00	0.00	0.00	1.00
MR2009a25	Parturition	Survived	1.00	0.00	0.11	0.89
MR2009a26	Parturition	Survived	1.00	0.00	0.11	0.89
MR2009a27	Parturition	Mortality	1.00	0.00	0.46	0.54
FO2016002	Parturition	Mortality	1.00	0.00	0.17	0.83
FO2016003	Parturition	Survived	1.00	0.00	0.00	1.00

FO2016004	Parturition	Survived	1.00	0.00	0.00	1.00
FO2016005	No Parturition		1.00	0.00	0.17	0.83
FO2016010	Parturition	Mortality	1.00	0.00	0.00	1.00
FO2016011	Parturition	Survived	1.00	0.00	0.00	1.00
FO2016012	Parturition	Mortality	1.00	0.00	0.00	1.00
FO2016014	Parturition	Mortality	1.00	0.00	0.00	1.00
FO2016015	No Parturition		1.00	0.00	0.00	1.00

[1]Individual IDs beginning with MR are from Middle Ridge herd and individual IDs beginning with FO are from Fogo Island herd.

[2] When parturition did not occur there was no calf mortality status.

Table C4. Parturition and calf status predictions predicted by the population-based method (PBM) from DeMars et al. (2013) for the 4-hour GPS fix interval for 19 calf-cow pairs from Middle Ridge and Fogo Island herd for which calf status was known. Predictions for Middle Ridge herd were generated by iteratively sampling of 4 out of the 7 females that could be used to generate parturition and calf mortality thresholds for the model and tested the on the remaining 6 individuals for all possible combinations. Predictions were pooled and the proportion of each prediction was calculated for every individual. Predictions for Fogo Island herd were generated by using 2 females that could be used to generate parturition and calf mortality thresholds for

the model and tested the on the remaining 7 individuals, thus an iterative process was not possible and the 2 individuals used to generate the event thresholds were not included in testing.

	Known Status		PBM Predictions (proportion of time each status was predicted)			
ID[1]	**Parturition**	**Calf Survival[2]**	**Parturition**	**No Parturition**	**Calf Mortality**	**Calf Survived[2]**
MR2009a01	Parturition	Survived	1.00	0.00	1.00	0.00
MR2009a04	Parturition	Survived	1.00	0.00	0.07	0.93
MR2009a06	Parturition	Mortality	1.00	0.00	0.43	0.57
MR2009a07	Parturition	Mortality	1.00	0.00	0.14	0.86
MR2009a08	Parturition	Survived	1.00	0.00	0.07	0.93
MR2009a09	Parturition	Survived	1.00	0.00	0.33	0.67
MR2009a16	Parturition	Survived	1.00	0.00	0.00	1.00
MR2009a25	Parturition	Survived	1.00	0.00	0.07	0.93
MR2009a26	Parturition	Survived	1.00	0.00	0.07	0.93
MR2009a27	Parturition	Mortality	1.00	0.00	0.43	0.57
FO2016002	Parturition	Mortality	TRUE	FALSE	TRUE	FALSE
FO2016005	No Parturition		FALSE	TRUE		
FO2016010	Parturition	Mortality	TRUE	FALSE	FALSE	TRUE
FO2016011	Parturition	Survived	TRUE	FALSE	FALSE	TRUE
FO2016012	Parturition	Mortality	TRUE	FALSE	FALSE	TRUE
FO2016014	Parturition	Mortality	TRUE	FALSE	FALSE	TRUE
FO2016015	No Parturition		TRUE	FALSE	TRUE	FALSE

[1]Individual IDs beginning with MR are from Middle Ridge herd and IDs beginning with FO are from Fogo Island herd.

[2] When parturition did not occur there was no calf mortality status and when parturition was not predicted there was no calf mortality status predicted.

Table C5. Parturition and mortality dates predicted from the individual-based (IBM) and population-based (PBM) method developed by DeMars et al. (2013) for 4-hour GPS fix interval for 43 GPS-collared females in Middle Ridge from 2009−2013. Individuals predicted to have had a parturition event by either or both models are included. Date format is YY-MM-DD.

		IBM		PBM	
ID	**Year**	**Parturition date**	**Mortality date**	**Parturition date**	**Mortality date**
MR2009a03	2009	09-06-06	09-06-18	09-05-24	
MR2009a06	2009	09-05-31	09-06-09	09-06-01	
MR2009a14	2009	09-05-27	09-06-03	09-05-23	
MR2009a17	2009	09-06-23	09-06-11	09-05-23	
MR2009a26	2009	09-06-01	09-06-25	09-05-23	
MR2009a27	2009	09-05-28	09-06-06	09-05-29	
MR2009a01	2009			09-05-23	
MR2009a02	2009			09-05-23	
MR2009a04	2009			09-05-23	
MR2009a07	2009			09-05-24	
MR2009a08	2009			09-05-23	
MR2009a09	2009			09-05-25	
MR2009a11	2009			09-05-23	
MR2009a13	2009			09-05-23	
MR2009a15	2009			09-05-23	
MR2009a16	2009			09-05-30	
MR2009a18	2009			09-05-23	
MR2009a21	2009			09-05-25	
MR2009a23	2009			09-05-23	
MR2009a24	2009			09-05-23	
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MR2009a09	2010	10-06-01	10-06-13	10-05-29	

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MR2009a24	2010	10-06-17	10-06-26	10-05-23	
MR2009a25	2010	10-06-18		10-05-23	
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MR2009a31	2010	10-05-28		10-05-23	
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MR2009a03	2010			10-05-26	
MR2009a04	2010			10-05-23	
MR2009a06	2010			10-05-23	
MR2009a08	2010			10-05-23	
MR2009a11	2010			10-05-23	
MR2009a14	2010			10-05-23	10-06-16
MR2009a16	2010			10-05-23	
MR2009a18	2010			10-05-25	
MR2009a21	2010			10-06-30	
MR2009a26	2010			10-05-23	
MR2009a27	2010			10-05-23	
MR2009a29	2010			10-06-04	
MR2009a03	2011	11-06-04	11-06-13	11-05-25	
MR2009a07	2011	11-05-29	11-06-03	11-05-23	
MR2009a08	2011	11-06-01	11-06-06	11-05-23	
MR2009a21	2011	11-05-29	11-06-02	11-05-24	
MR2009a31	2011	11-05-26	11-06-26	11-05-24	
MR2011a01	2011	11-06-06	11-06-13	11-06-08	
MR2011a02	2011	11-05-27	11-06-10	11-05-29	
MR2011a03	2011	11-05-27	11-06-04	11-05-28	
MR2011a04	2011	11-05-27	11-06-08	11-05-23	
MR2011a06	2011	11-05-30	11-06-06	11-05-23	

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MR2009a10	2011			11-05-31	
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MR2009a14	2011			11-05-23	
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MR2009a27	2011			11-05-23	
MR2009a28	2011			11-05-23	
MR2009a30	2011			11-05-23	
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MR2010a03	2011			11-05-23	
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MR2009a18	2012	12-06-04	12-06-09	12-05-29	
MR2009a28	2012	12-05-25	12-05-31	12-05-25	
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MR2009a10	2012			12-05-27	
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MR2009a21	2012			12-05-29	
MR2009a25	2012			12-05-25	
MR2009a26	2012			12-05-23	

MR2009a30	2012			12-05-26	
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MR2011a01	2013			13-05-23	13-05-30
MR2012a02	2013			13-05-23	
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MR2012a04	2013			13-05-23	
MR2012a05	2013			13-05-29	

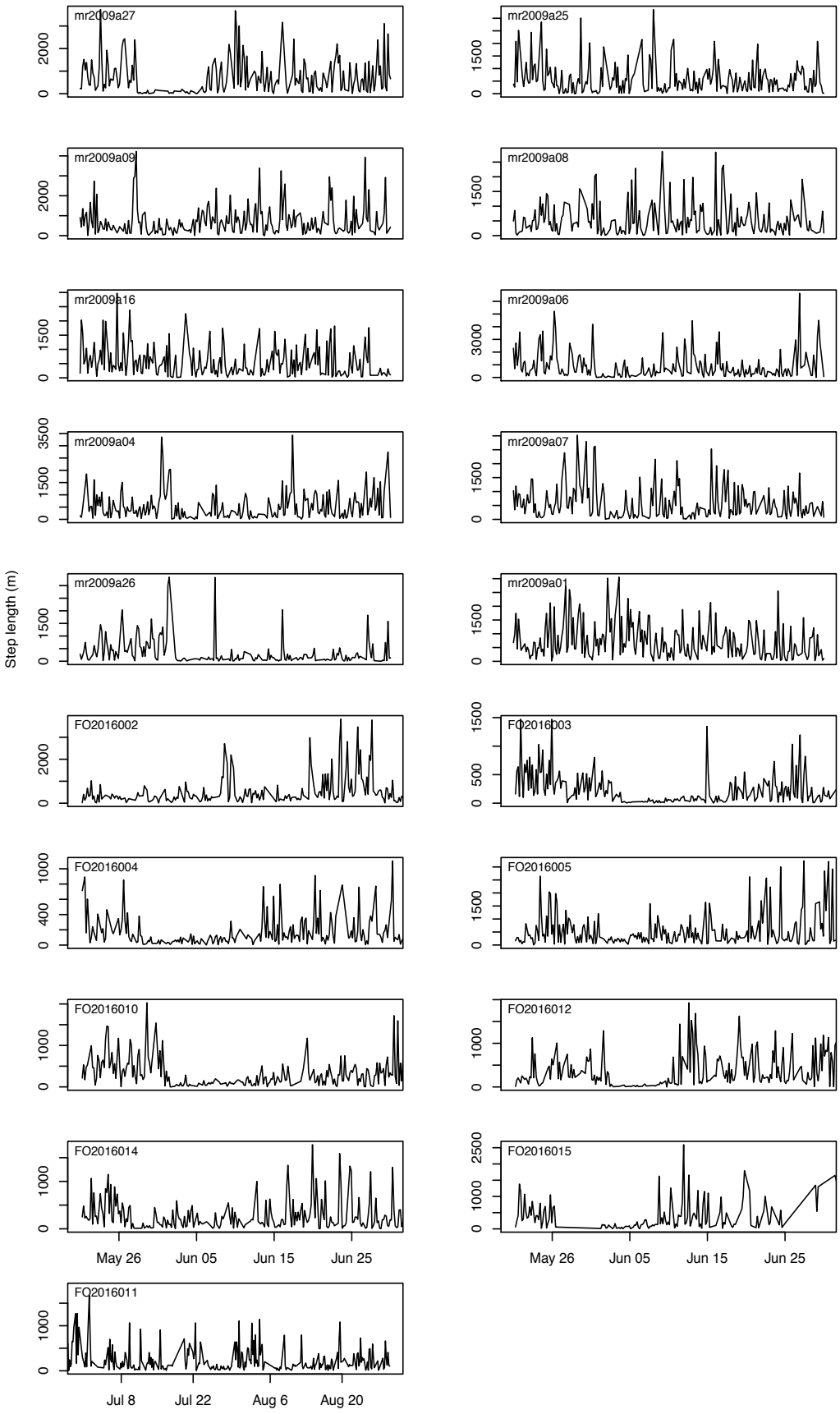
Step length (m)
mr2009a27
mr2009a25
mr2009a09
mr2009a08
mr2009a16
mr2009a06
mr2009a04
mr2009a07
mr2009a26
mr2009a01
FO2016002
FO2016003
FO2016004
FO2016005
FO2016010
FO2016012
FO2016014
FO2016015
FO2016011
May 26
Jun 05
Jun 15
Jun 25
Jul 8
Jul 22
Aug 6
Aug 20

Figure C1. Time-series of step lengths for the 19 calf-cow pairs from Middle Ridge herd and Fogo Island herd for the 4-hour GPS fix interval. I tested my methods over the time interval 21 May – 30 July for every individual in the Middle Ridge herd and 8 individuals in the Fogo Island herd. I tested my methods over the time interval 30 May – 30 August for one individual to account for a record-late birth in the Fogo herd in 2016 (Bonar et al. 2017).

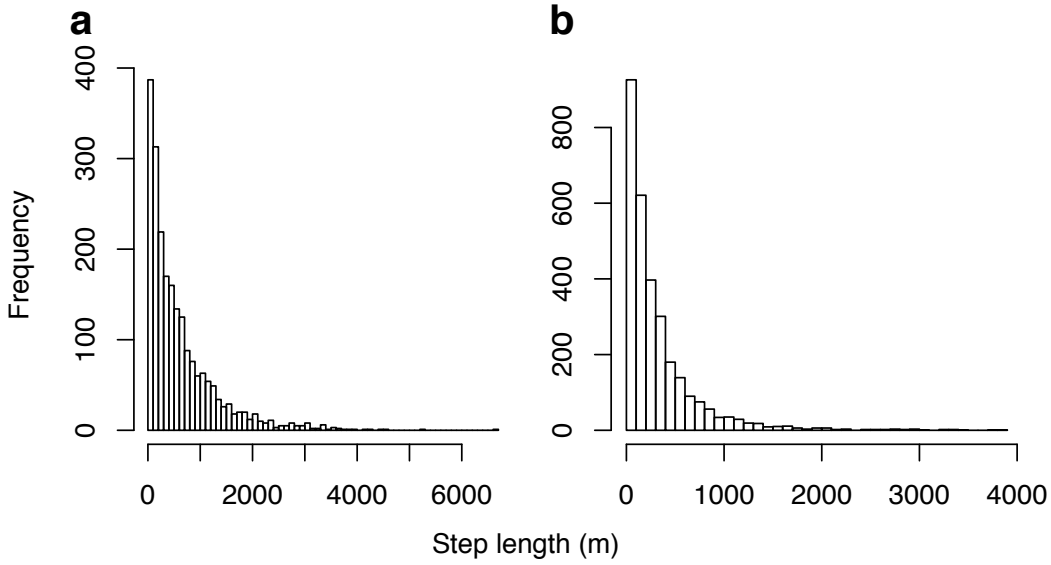

Figure C2. Distribution of step lengths for the 19 calf-cow pairs from Middle Ridge herd and Fogo Island herd for the 4-hour GPS fix interval. Both herds fit the assumption of exponentially distributed step lengths (DeMars et al. 2013).

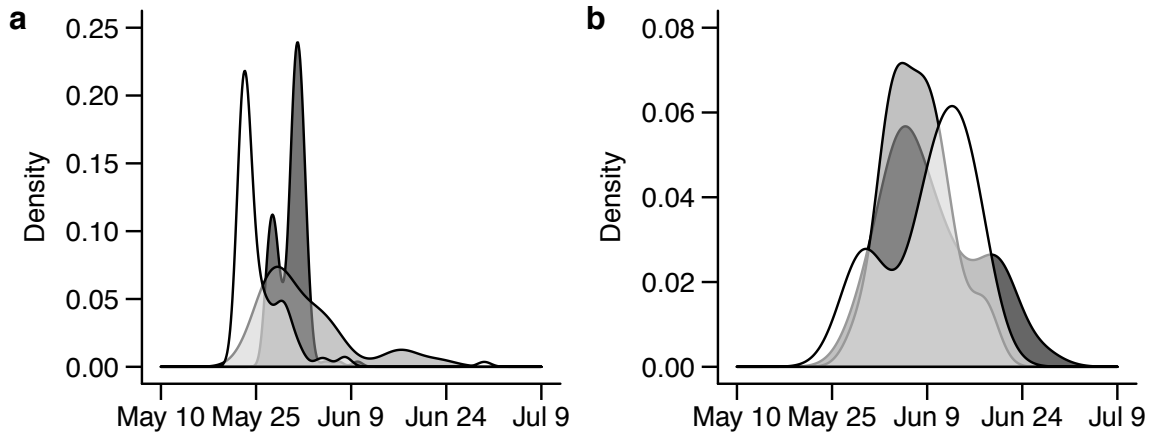

Figure C3. Comparison of density distributions of herd-wide VHF calf collaring dates and mortality dates from (Ellington et al. 2017) with estimated parturition and calf mortality dates derived from DeMars et al. (2013) individual-based method (IBM) and population-based method (PBM) at the 4-hour GPS fix interval for 43 adult females from Middle Ridge herd between 2009–2013 (a) Density distributions of herd-wide VHF calf collaring dates (dark gray), estimated parturition dates derived from IBM (light gray) and PBM (white). (b) Density distributions of herd-wide VHF calf mortality dates (dark gray), estimated calf mortality dates derived from IBM (light gray) and PBM (white).

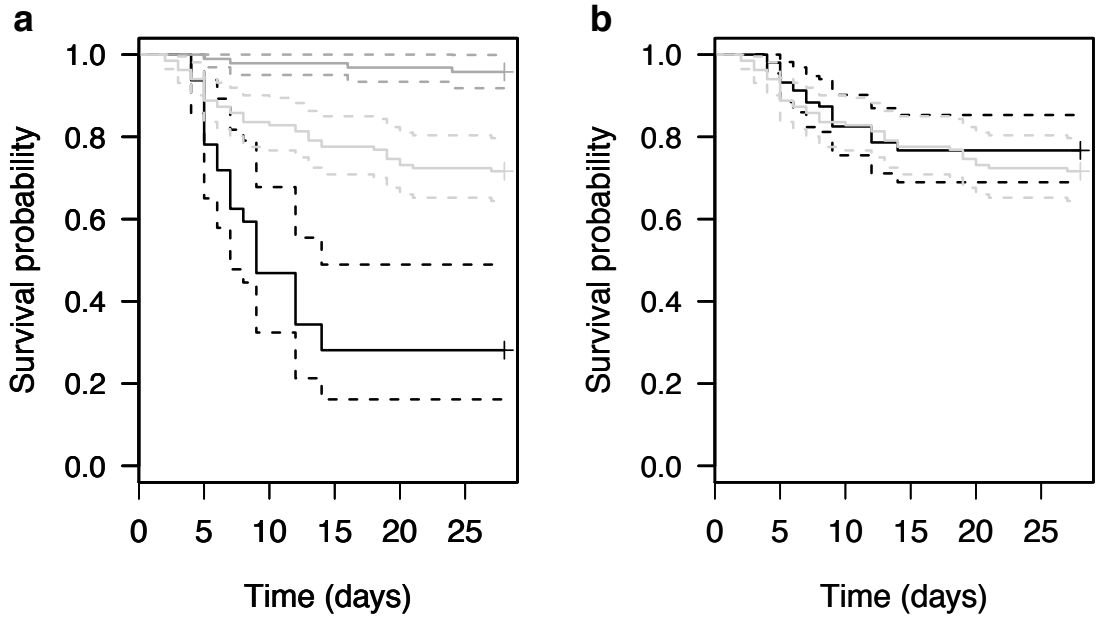

Figure C4. (a) Kaplan-Meier survival probability curves comparing survival data generated at the 4-hour GPS fix interval for 43 GPS-collared females in Middle Ridge from 2009−2013 using DeMars et al.'s (2013) individual-based method (IBM; black), and population-based method (PBM; dark gray), and calf mortality from 134 VHF-collared calves in Middle Ridge from 2009−2013 (light gray). Dotted lines are 95% confidence intervals. (b) Kaplan-Meier survival probability curves comparing calf mortality data from 134 VHF-collared calves from Middle Ridge herd from 2009−2013 (light gray) to survival data generated by using a combination of the IBM and PBM models for 43 GPS-collared females in Middle Ridge herd from 2009−2013 (black). Parturition was determined for 43 GPS collared females from 2009–2013 using the PBM and then calf loss was determined using the IBM. For calves whose parturition was predicted using the PBM, if the IBM did not predict calf loss before four weeks I assumed the calf survived.

APPENDIX D. CHAPTER 3 SUPPLEMENTARY FIGURES AND TABLES

D.1 Supplementary Tables

Table D1. Table of values for broken stick linear regressions of ranked seasonal average nearest neighbour (NN) distance for n = 43 adult female caribou (*Rangifer tarandus*) in Newfoundland, Canada (101 caribou-years) from 2009-2013.

Year	Coefficient	β Estimate ± SE	t-value	p-value
2009	Intercept	13.95 ± 0.66	21.15	<0.001
	ID (line 1)	0.37 ± 0.07	5.12	<0.001
	ID (line 2)	5.03 ± 0.30	16.81	NA
	Break-point	15.90 ± 0.22		
2010	Intercept	14.99 ± 1.08	13.87	<0.001
	ID (line 1)	0.55 ± 0.09	5.80	<0.001
	ID (line 2)	13.21 ± 1.60	8.24	NA
	Break-point	19.57 ± 0.21		
2011	Intercept	16.15 ± 0.60	26.75	<0.001
	ID (line 1)	0.32 ± 0.05	6.59	<0.001
	ID (line 2)	15.33 ± 0.94	16.22	NA
	Break-point	21.64 ± 0.11		
2012	Intercept	12.30 ± 0.75	16.46	<0.001
	ID (line 1)	1.04 ± 0.08	13.52	<0.001
	ID (line 2)	3.41 ± 0.64	5.31	NA
	Break-point	16.50 ± 0.48		
2013	Intercept	27.42 ± 0.84	32.64	<0.001
	ID (line 1)	0.51 ± 0.14	3.78	0.004
	ID (line 2)	1.65 ± 0.57	2.91	NA
	Break-point	10.33 ± 0.94		

D.2 Supplementary Figures

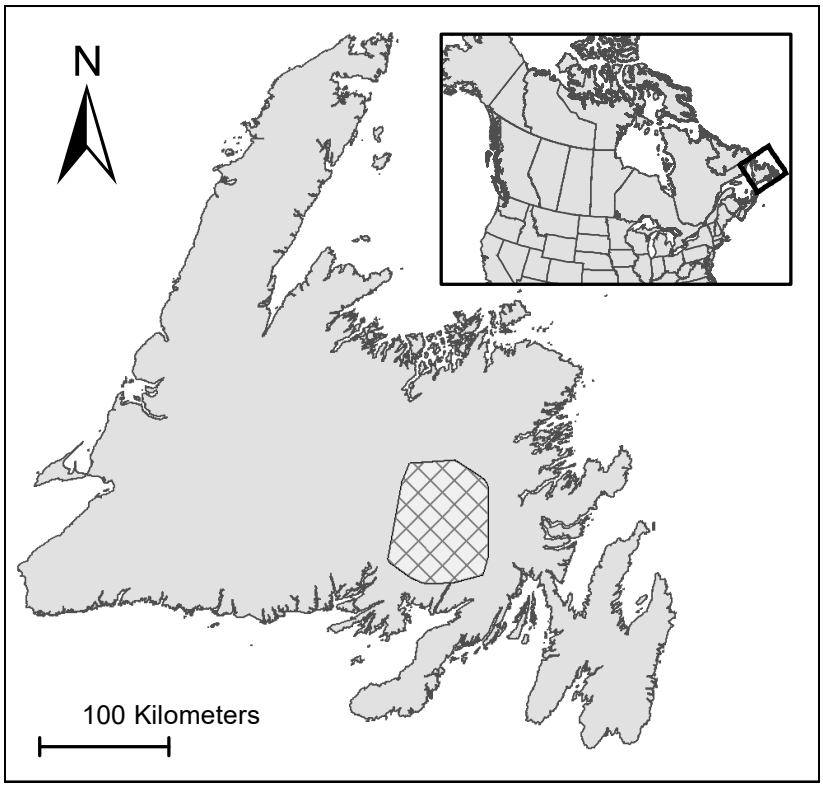

Figure D1. Map of study area in Newfoundland, Canada, with the location of Middle Ridge caribou (*Rangifer tarandus*) herd used for data collection between 2009 and 2013.

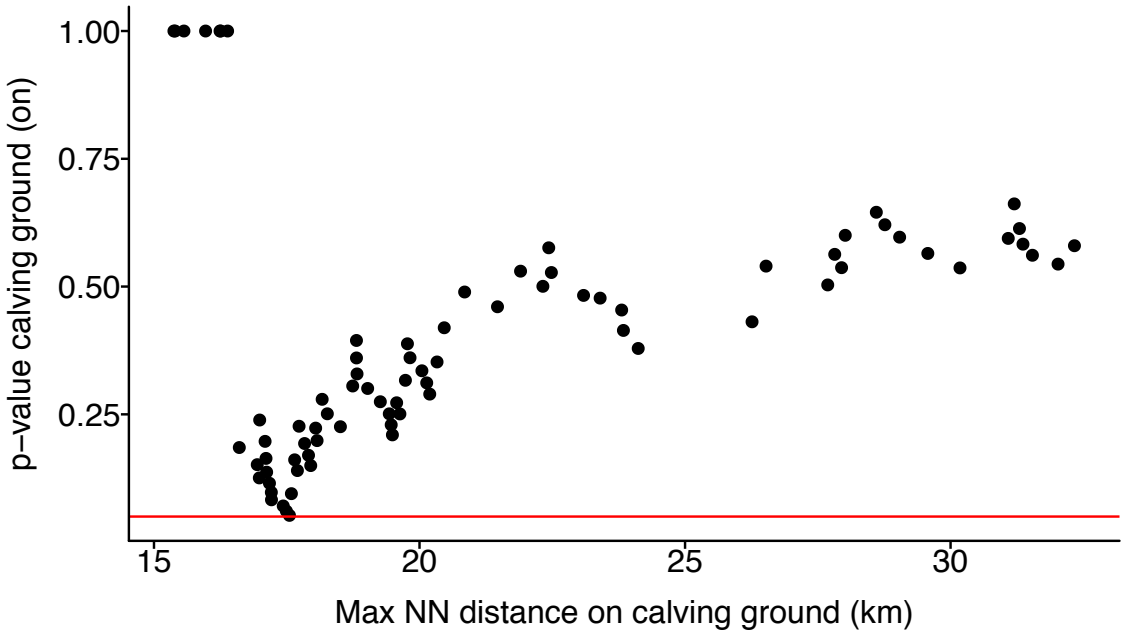

Figure D2. Resulting p-values from the generalized linear mixed model testing the relationship between calf loss and position on the calving ground (on/off) for 43 adult female caribou (*Rangifer tarandus*) in Newfoundland, Canada (n = 101 caribou-years) with random variables of ID and year. I generated p-values for the fixed effect calving ground (on/off) after sequentially removing the individual with the largest seasonal average nearest neighbour (NN) distance on the calving ground and revaluating the effect of seasonal average NN distance on calf survival for adult females on and off the calving ground. Red line indicates p = 0.05. The NN distance at which the p-value was the lowest (p = 0.052) was 17.55km.

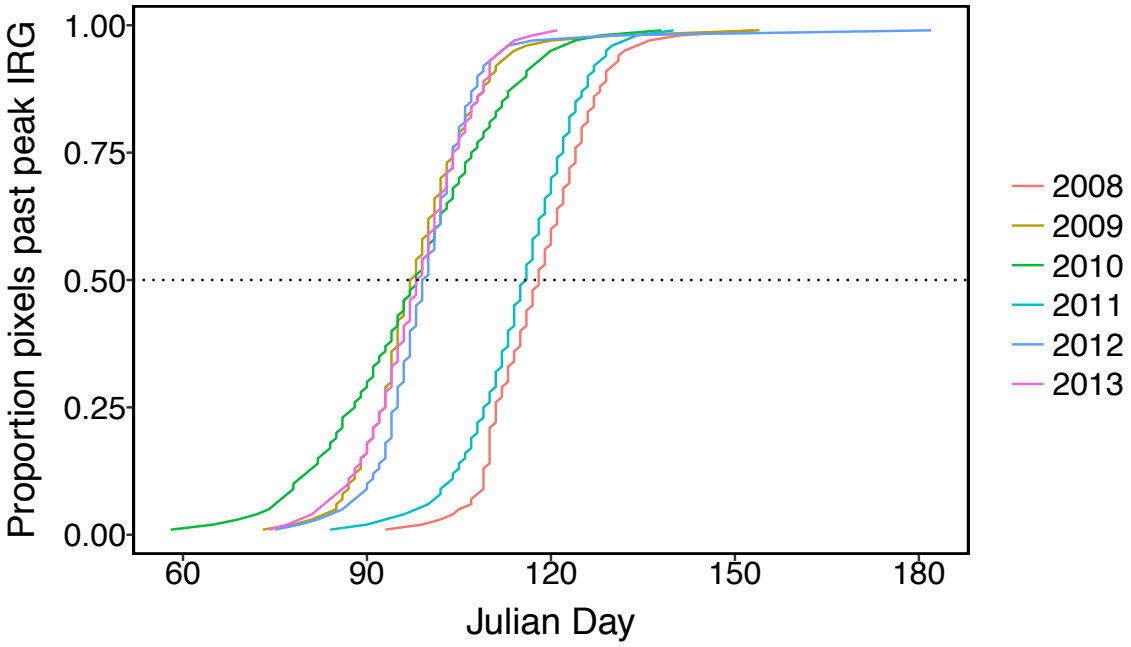

Figure D3. Plot of green-up curves for Middle Ridge caribou (*Rangifer tarandus*) herd in Newfoundland, Canada. The proportion of pixels that were peak incidental rate of green-up (IRG) is plotted as a function of Julian day for the years 2008 – 2013. The dotted line indicates the median number of pixels that passed peak IRG.